CATARINA DE LOURDES ARAÚJO SILVA

TAXONOMY, SYSTEMATICS, MORPHOLOGICAL AND MOLECULAR PHYLOGENY OF THE ORDER TANAIDACEA (CRUSTACEA: PERACARIDA), FROM THE ANTARCTIC, ATLANTIC AND PACIFIC OCEANS

Tese de Candidatura ao grau de Doutor em Ciências Biomédicas submetida ao Instituto de Ciências Biomédicas Abel Salazar da Universidade do Porto.

Orientador: Doutor Kim Larsen

Coorientadora: Doutora Elsa Froufe
Investigadora auxiliar
Laboratório de Ecologia Aquática e Evolução, Centro Interdisciplinar de Investigação Marinha e Ambiental

Coorientador: Doutor João Coimbra
Professor Emérito
Instituto de Ciências Biomédicas Abel Salazar da Universidade do Porto

Esta tese foi financiada por uma bolsa de doutoramento da Fundação CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), nº do Processo: 5428/10-6.

À minha família.

“...Sei que há léguas a nos separar

Tanto mar, tanto mar

Sei, também, como é preciso,

Navegar, navegar...”

Tanto Mar (Chico Buarque de Holanda)

AGRADECIMENTOS

Em primeiro, tenho muito a agradecer aos meus Pais, Paulo e Cássia, por sempre acreditarem e incentivarem em todas as minhas decisões. Amo muito vocês. Obrigada Painho e Mainha!

Ao meu orientador Dr. Kim Larsen, por todo aprendizado e por ter confiado em mim.

À minha coorientadora Dr. Elsa Froufe (CIIMAR/LAEE), por me orientar, ter tido paciência com a ajuda nas análises moleculares, na escrita e pelas tantas discussões construtivas, sejam de "puxões de orelha" e incentivos ao mundo da genética molecular. Seus ensinamentos não serão esquecidos!! :)

Ao Professor Emérito João Coimbra, por ter aceite ser coorientador deste trabalho, e pela confiança que demonstrou neste projecto.

À Fundação CAPES pelo financiamento desta tese de doutoramento.

Ao Professor Dr. Paulo Jorge Parreira dos Santos (Universidade Federal de Pernambuco/UFPE/Brasil), por ter aceite ser o tutor no Brasil deste doutoramento.

À Professora Dr. Angelika Brandt (University of Hamburg) por ter concedido o material do Programa ANDEEP I-III.

Ao Professor Dr. Jesser Souza-Filho (Universidade Federal de Pernambuco/Brasil), por ter concedido o material do Programa REVIZEE-NE, depositado no Museu de Oceanografia Petrônio Alves Coelho.

Aos Dr. Lenaick Menot (IFREMER) and Dr. Carsten Rühlemann (BGR), por ter concedido o material da Campanha BIONOD/2012.

À Dr. Karen Osborn (Smithsonian Institution, D.C., USA) por me receber e disponibilizar a coleção de Tanaidacea utilizada nas análises taxonômicas desta tese.

Aos colegas de laboratório Allan Souza, Martina Ilarri e Ester Dias, pelos momentos de descontração.

À amiga Débora Lucatelli (Universidade Federal de Pernambuco/Brasil), por estar sempre ao meu lado, ter me ajudado nos momentos de angústia, e principalmente, com a ajuda na edição final da tese. Obrigada por tudo! :)

De acordo com o disposto do nº 2, alínea a, do artigo 31º do Decreto Lei nº 230/2009, utilizaram-se neste trabalho resultados já publicados ou em vias de publicação. Em todos estes trabalhos a candidata participou na obtenção, análise e discussão dos resultados, bem como na elaboração da sua forma publicada, que a seguir se enumeram:

Article 1. Araújo-Silva, C.L. & Larsen, K. (2012a). Tanaidacea from Brazil. III. New records and description of a new species collected from REVIZEE-NE Program. *Nauplius*, 20 (2): 87–105.

Article 2. Araújo-Silva, C.L. & Larsen, K. (2012b). Tanaidacea (Tanaidacea: Crustacea) from Brazil. IV. A new genus and two new species from the family Leptocheliidae. *Zootaxa*, 3523: 1–19.

Article 3. Araújo-Silva, C.L., Coelho, P.A.† & Larsen, K. (2013). Tanaidacea (Peracarida) from Brazil. V. Two New Species of *Apseudes* Leach, 1814 from the Northeastern Coast of Brazil. *Crustaceana*, 86 (2) 221–245.

Article 4. Larsen, K. & Araújo-Silva, C.L. (2014a). A new genus of Colletteidae (Crustacea: Peracarida: Tanaidacea) from the Pacific with comments on dimorphic males with species specific characters. *Journal of the Marine Biological Association of the United Kingdom*, 94 (5): 969–974.

Article 5. Araújo-Silva, C.L., Froufe, E. & Larsen, K. (2015). Two new species of family Neotanaidae (Peracarida: Tanaidacea) from the Antarctic and Mid-Pacific Oceans. *Zootaxa*, 4018 (4): 535–552.

Article 6. Larsen, K. & Araújo-Silva, C.L. (2014b). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited III: the family Akanthophoreidae. *Zootaxa*, 3796 (2): 237–264.

Article 7. Araújo-Silva, C.L., Larsen, K. & Froufe, E. (submitted). Tanaidacea (Crustacea: Peracarida) systematics revisited: A combination of morphological and molecular approaches. *Organisms Diversity & Evolution*.

INDEX

LIST OF FIGURES

LIST OF TABLES

LIST OF APPENDIX

ABSTRACT

Tanaidaceans are small peracarid crustaceans, found mainly in the marine habitat, from the intertidal zone to the deep-sea. In these areas, they can be very abundant but because their systematics is still dubious, they have been often neglected in ecological and biodiversity studies.

The purpose of this thesis was to improve the knowledge of the order Tanaidacea and several issues related to the taxonomic, systematics, morphological and molecular phylogenies have also been addressed. In order to do that, samples from the Atlantic (Brazilian coast [REVIZEE-NE program]), Antarctic Ocean (ANDEEP I-III program) and Pacific Ocean (BIONOD/2012 campaign) were examined and analyzed using both morphological and molecular methods. Three hundred and forty nine individuals of Tanaidacea were identified and subsequently placed in 16 families, 43 genera and 61 species. Of these, three genera and eleven species new to science have been fully described and illustrated. A further 22 taxa had their geographic distribution expanded for the first time in their respective study areas. The phylogenetic status of the family Akanthophoreidae was revisited by a morphological phylogenetic analysis by using a matrix of 103 characters, which confirms that this family is monophyletic.

The current suborders classification of Tanaidacea was revisited through the combine of both morphological and molecular datasets. In order to do that, 112 morphological characters were examined. Also, total DNA was extracted from 17 species, which resulted in 45 new sequences of three different genes: one mitochondrial cytochrome *c* oxidase (COI), one nuclear Histone 3 (H3), and one nuclear large subunit ribosomal DNA (28S rRNA). Phylogenetic analyses were conducted using both molecular and morphological datasets. These allowed to presente a new classification in the Tanaidacea suborders by recognizing four suborders: Apseudomorpha, Neotanaidomorpha (re-erected), Tanaidomorpha and Paratanaidomorpha (new suborder) rather than the currently accepted two.

Of the taxa mentioned above, 80 specimens were collected from the Atlantic and are placed in seven families, nine genera, and ten species. The new genus, *Makraleptochelia* and five of the new species: *Apseudes aisoe, A. noronhensis, Makraleptochelia potiguara, Intermedichelia jesseri,* and *Paratanais coelhoi* were described from this area. Four genera: *Apseudes*, *Biarticulata*, *Nototanoides* and *Arhaphuroides,* were recorded for the first time also from this area. The suborder Paratanaidomorpha was the most representative suborder in this area.

From the Antarctic Ocean a total of 152 specimens were analyzed and placed in eleven families, 24 genera and 36 species. The new genus, *Parakanthophoreus*, and four of the new species: *Neotanais bicornutus*, *Chauliopleona ciimari, C. andeepi,* and *Parakanthophoreus greenwichius,* were collected from this area. Six other taxa, *Tanaella kroyeri, Tanaella* cf. *prolixcauda, Armaturatanais, Parafilitanais, Portaratrum* and *Insociabilitanais*, were recorded from this area for the first time. Paratanaidomorpha was the most representative suborder.

Finally, from the Pacific Ocean a total of 117 specimens were analyzed and placed in ten families, 35 genera, and 41 species. The new genus, *Cheliasetosatanais,* and two new species, *Venusticrus thor* and *C. spinimaxillipedus*, were collected from this area. A further eight taxa, *Glabroapseudes, Venusticrus, Paraiungentitanais, Armaturatanais, Caudalonga, Leptognathiella, Insociabilitanais* and *Pulcherella*, were recorded from this area for the first time. Four other genera, *Leviapseudes, Parafilitanais, Portaratrum,* and *Paratyphlotanais*, are first records from the North Pacific. The suborder Paratanaidomorpha was also the most representative suborder in this area.

From the morphological observations of those new described species, it was proposed to transfer the genus *Intermedichelia* from *incertae sedis* to family Leptocheliidae; to consider the genus *Muramurina* a junior synonym of *Apseudes*; and to transfer *Neotanais rotermundiae* to genus *Venusticrus*.

The morphological phylogenetic revision of the family Akanthophoreidae suggests that this family is monophyletic and forms a clade including the genera: *Akanthophoreus, Chauliopleona, Mimicarhaphura, Parakanthophoreus*, *Paraleptognathia, Stenotanais,* and *Tumidochelia*. The genus *Gejavis,* however, is removed from the family and placed to genus *incertae sedis*.

The current systematics classification of Tanaidacea suborders was revisited. In order to do that, it was included several members of the current suborders: Tanaidomorpha and Apseudomorpha. This was addressed through phylogenetic analyses obtained from both morphological and molecular data, separately as well as combined. Ten new morphological characters were added to the matrix of 102 characters and 45 new sequences of three genes from 17 species were obtained for the phylogenetic analyses. These analyses found the superfamilies Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea monophyletic and supported by their own synapomorphy. Based on these results a new suborder classification for the Tanaidacea is presented: 1) Neotanaidomorpha is re-erected to suborder encompassing the superfamily Neotanaoidea; 2) Tanaidomorpha (*sensu* Kakui *et al*. 2011) is restricted to include only the superfamily Tanaoidea; and 3) The superfamily Paratanaoidea is removed from Tanaidomorpha and raised to suborder rank as Paratanaidomorpha (new suborder). Further results from these phylogenetic analyses also presented changes in the families Colletteidae and Typhlotanaidae. Colletteidae is polyphyletic and the genus *Caudalonga* is placed as *incertae sedis*, while the genus *Insociabilitanais* is transferred from *incertae sedis* to Typhlotanaidae.

RESUMO

Os Tanaidacea são pequenos crustáceos pertencentes à superordem Peracarida, que vivem principalmente em habitats marinhos, desde as zonas intertidais até às regiões de grande profundidade, onde podem ser abundantes. No entanto, estes animais têm sido frequentemente negligenciados em estudos ecológicos e de biodiversidade, devido a indefinições quanto à sua sistemática.

Esta tese teve como objetivo principal ampliar o conhecimento sobre a ordem Tanaidacea, ao abordar a sua taxonomia, sistemática e filogenias morfológica e molecular. Com este objetivo, foram examinadas e analisadas através de abordagens morfológicas e moleculares, amostras recolhidas nos Oceanos Atlântico (Costa Brasileira, Programa REVIZEE-NE), Antártico (Programa ANDEEP I-III) e Pacífico (Campanha BIONOD/2012). Foram identificados e classificados trezentos e quarenta e nove indivíduos de Tanaidacea em 16 famílias, 43 géneros e 61 espécies. Destes indivíduos, três géneros e onze novas espécies foram devidamente descritas e ilustradas. Adicionalmente, a distribuição geográfica de 22 dos taxa examinados foi revista e ampliada. A posição filogenética da família Akanthophoreidae foi investigada usando uma matriz morfológica com 103 caracteres. Os resultados desta análise filogenética confirmaram a monofilia desta família.

A classificação atual das subordens de Tanaidacea foi também investigada através da combinação de dados morfológicos e moleculares. No total, 112 caracteres morfológicos foram usados. O ADN foi extraído de 17 espécies, resultando em 45 novas sequências pertencentes a três genes diferentes: um mitocondrial, citocromo *c* oxidase (COI), e dois nucleares, Histona 3 (H3) e subunidade ribossomal (28S). As análises filogenéticas efetuadas através dos dados morfológicos e moleculares, permitiram propor uma nova classificação das subordens existentes de Tanaidacea. Assim sendo, ao invés das duas subordens reconhecidas até à presente tese, aqui são reconhecidas quatro subordens: Apseudomorpha, Neotanaidomorpha (elevada), Tanaidomorpha e Paratanaidomorpha (nova subordem).

Dos taxa acima mencionados, foram amostrados 80 espécimes no Atlântico que foram classificados em sete famílias, nove géneros e dez espécies. Para esta região, a subordem Paratanaidomorpha foi a subordem mais representativa, além de ter sido descrito o novo género *Makraleptochelia,* cinco espécies novas *Apseudes aisoe, A. noronhensis, M. potiguara, Intermedichelia jesseri,* e *Paratanais coelhoi*, e quatro géneros aí registrados pela primeira vez: *Apseudes*, *Biarticulata*, *Nototanoides* e *Arhaphuroides*.

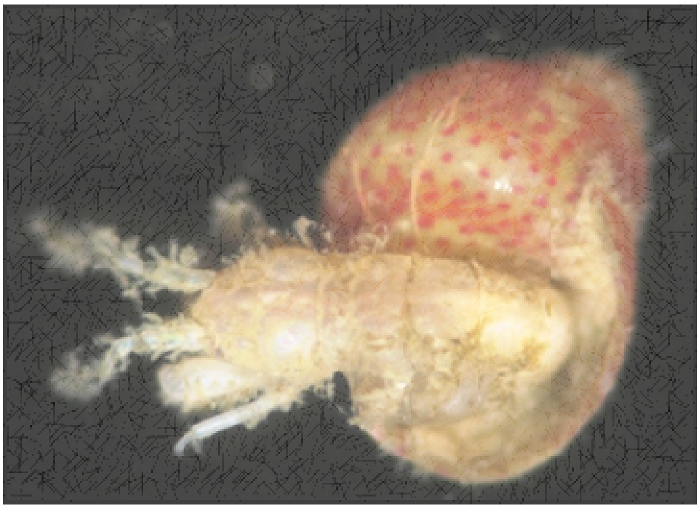
Do Oceano Antártico, um total de 152 espécimes foram analisados e classificados em onze famílias, 24 géneros e 36 espécies, tendo sido Paratanaidomorpha a subordem mais representativa, bem como um novo género, *Parakanthophoreus*, e quatro novas espécies foram descritas: *Neotanais bicornutus*, *Chauliopleona ciimari, C. andeepi,* e *P. greenwichius*. Outros seis taxa, *Tanaella kroyeri, Tanaella* cf. *prolixcauda, Armaturatanais, Parafilitanais, Portaratrum* e *Insociabilitanais*, foram registrados para esta área pela primeira vez.

Finalmente, para o Oceano Pacífico um total de 117 espécimes foram examinados e classificados em dez famílias, 35 géneros e 41 espécies. O novo género *Cheliasetosatanais*, e duas novas espécies, *Venusticrus thor* e *C. spinimaxillipedus*, foram amostrados nesta área. Oito géneros, *Glabroapseudes, Venusticrus, Paraiungentitanais, Armaturatanais, Caudalonga, Leptognathiella, Insociabilitanais* e *Pulcherella*, foram registrados neste Oceano pela primeira vez. Além disto, outros quatro géneros, *Leviapseudes, Parafilitanais, Portaratrum* e *Paratyphlotanais*, tiveram os seus primeiros registros para o Norte do Pacífico. Paratanaidomorpha foi a subordem mais representativa para esta área.

As observações morfológicas realizadas nas onze espécies novas descritas nesta tese resultaram: na transferência do género *Intermedichelia* de *incertae sedis* para a família Leptocheliidae; à invalidação do género *Muramurina* como sinónimo júnior de *Apseudes*; e na transferência da espécie *Neotanais rotermundiae* para o género *Venusticrus*.

A revisão filogenética da família Akanthophoreidae, sugere que esta família é monofilética, formando um clado que inclui os géneros: *Akanthophoreus,* *Chauliopleona, Mimicarhaphura, Parakanthophoreus*, *Paraleptognathia, Stenotanais* e *Tumidochelia*. O género *Gejavis* foi removido desta família e classificado como género *incertae sedis*.

A sistemática atual das subordens de Tanaidacea foi também investigada através de análises filogenéticas, usando uma combinação de dados morfológicos e moleculares e também individualmente. Dez novos caracteres morfológicos foram adicionados à matriz de 102 caracteres; e 45 novas sequências obtidas de 17 espécies (três genes). Estas análises encontraram as superfamílias Paratanaoidea, Tanaoidea, Neotanaoidea e Apseudoidea monofiléticas e bem suportadas, cada uma com a sua sinapomorfia. Baseado nestes resultados uma nova classificação é aqui apresentada: 1) Neotanaidomorpha foi novamente elevada a subordem e inclui agora a superfamília Neotanaoidea; 2) Tanaidomorpha (*sensu* Kakui *et al*. 2011) é aqui restringida incluindo apenas a superfamília Tanaoidea; 3) a superfamília Paratanaoidea foi removida de Tanaidomorpha e elevada a subordem como Paratanaidomorpha (nova subordem). Além destes resultados, as análises filogenéticas também levaram a mudanças dentro das famílias Colletteidae e Typhlotanaidae. Colletteidae é polifilética e o género *Caudalonga* foi classificado como *incertae sedis*, enquanto o género *Insociabilitanais* foi transferido de *incertae sedis* para Typhlotanaidae.



CHAPTER I. GENERAL INTRODUCTION

1. GENERAL INTRODUCTION

1.1. An overview of tanaidacean biology

The superorder Peracarida Calman, 1904 comprises approximately one-third of all extant crustaceans (Spears *et al*. 2005). This superorder is considered one of the most wide-spread and adapted groups among crustaceans and can be found from terrestrial areas to the deep-sea. They are commonly termed "crustacean marsupials" because the females develop a brood-pouch where they carry the eggs and first larval stage. The brood-pouch can be formed by two different structures called oostegites and ovisacs. Peracarids display direct development, meaning that the larvae develop into an adult, without free-swimming *nauplius* stages. The peracarids currently encompass nine extant orders (Martin & Davis 2001) and among these is the Tanaidacea Dana, 1849.

Tanaidaceans are usually small, ranging from 1 mm (e.g. *Pseudotanais* Sars, 1882) to 75 mm (e.g. *Gigantapseudes* Gamo, 1984), although most species reach only a few millimeters in length. According to Anderson (2013) and the World Register of Marine Species website (WoRMS - December 2015), the Tanaidacea encompass 38 families, 280 genera and 1,260 species.

Tanaidaceans are found mainly in the marine habitat, from the intertidal zone to the deep-sea, but there are also a few records from brackish and freshwater habitats (Larsen & Hansknecht 2004). They are exclusively benthic and occur in most habitats, and as such may be considered a eurytopic group (Błażewicz-Paszkowycz *et al.* 2012). Tanaidaceans can be very abundant and can reach high densities in some areas. *Allotanais hirsutus* (Beddard, 1886) for instance, can reach densities of 56,000 ind/m^2 or in extreme cases up to 146,000 ind/m^2 (Delille *et al*. 1985). Particularly in the abyssal region are the Tanaidacea one of the most abundant and diverse components of the macrofauna, and to a lesser degree of the meiofauna (Sokolova 1972). The Tanaidacea can comprise up to 19% of the macrofauna in the deep-sea, where it frequently is the second most abundant peracarid order (Wolff 1977; Borowski 2001).

They can be found in many different habitats: on hard substrates (Spaccesi & Capítulo 2012) such as sandstones (Araújo-Silva & Larsen 2012a), directly on rock surfaces (Borthagaray & Carranza 2007), on corals (Sieg & Zibrowius 1988), on or within sponges (Araújo-Silva & Larsen 2012a; Klitgaard 1995), or on bryozoan colonies (Hassack & Holdich 1987). In soft substrates, they are recorded from habitats of all sediment sizes (Bamber & Sheader 2005). They are also recorded from many special habitats, such as estuarine wetlands (Wang *et al*. 2010), underwater caves (Guţu & Iliffe 1985), mangrove swamps (Drumm 2003), algae habitats (Araújo-Silva & Larsen 2012a) among others. Finally, they can also be associated with natural anoxic habitats (Sieg & Heard 1985), hydrothermal vents, 'cold seeps' (Larsen 2006), mud volcanoes (Larsen *et al*. 2006), or associated with sunken wood (Larsen 2006; Błażewicz-Paszkowycz *et al.* 2014).

This group interacts with other organisms in many different ways. They are recorded living within gastropod shells (Messing 1983), on oysters shells (Bamber & Bird 1997), inside the body cavity (parasitic) of polychaetes (Suárez-Morales *et al*. 2011) and of holothurians (Thurston *et al*. 1987), or as epifauna on turtles (Caine 1986) and manatees (Morales-Vela *et al*. 2008).

In contrast to many other crustaceans (e.g. decapods, euphausiaceans), tanaidaceans do not play any direct economic roles. However, they are known to be a very significant component of the diet of several commercial important species. For instance, *Monokalliapseudes schubartii* (Mañe-Garzon, 1949) is frequently consumed by the larvae of a number of marine fishes (e.g. *Micropogonias furnieri* (Desmarest, 1823), *Odontesthes bonariensis* (Cuvier & Valenciennes, 1835) (Gnewuch & Crocker 1985). Tanaidaceans are also consumed by estuarine decapods (e.g. *Farfantepenaeus paulensis* (Pérez Farfante, 1967), *Callinectes sapidus* MJ Rathbun, 1896 (Montagnolli *et al*. 2004). In addition, they can also have a significant influence on some macrobenthos communities by consuming the larvae and juveniles of other species (Highsmith 1983; Oliver & Slattery 1985).

Tanaidaceans deploy a number of different feeding strategies. Most species are known to be detritivores, scavengers, or browsers (Drumm 2005). Some studies of gut contents have indicated that some species can also be raptorial carnivores, preying on nematodes, copepods, echinoid larvae, polychaetes as well as other small invertebrates (Larsen 2005). Larger prey can also be consumed (Larsen *et al*. 2015) but this feeding mode is probably restricted to a few larger species. Some species of Apseudomorpha also employ a filter feeding strategy

(Drumm 2005). In the deep-sea, they are hypothesized to consume large numbers of Foraminifera (Larsen 2005).

Identifying tanaidaceans is very difficult. Firstly because of their small size and the often challenging requiring dissections of minute mouthparts; secondly because of the still confusing systematics; thirdly because of their ontogenetic variations; fourthly and most importantly because of their many different reproductive strategies. These reproductive strategies can involve either separate sexes or hermaphroditism and some are even suggested to be parthenogenetic although this is not confirmed (Sieg 1983). The question of hermaphroditism is further divided in to two types: simultaneous- when the individuals are found with both a penal cone and oostegites, or sequential- when the individuals changes sexes from female to male, termed protogynic (Kakui & Hiruta 2014; Rumbold *et al*. 2015). A result of protogynic hermaphroditism is male polymorphism where the presence of several different morphs obstructs identification (Sieg 1983).

1.2. Tanaidacea distribution

Tanaidaceans are widely distributed, being found at all latitudes from the polar regions to the tropics (Larsen 2005). The wide distribution of several species is still under discussion as tanaidaceans are known to have limited dispersal capacity and lacks a pelagic dispersal stage (Larsen 2005; Błażewicz-Paszkowycz 2007).

Although tanaidaceans have limited swimming abilities, many shallow water taxa have been found using other mechanisms to disperse. They have been recorded floating on the surface during the nocturnal tidal movements where they may be passively dispersed by the currents (Saigusa & Oishi 2000), rafting on algae (Sieg 1980), as epifauna or fouling on objects such as ship hulls (Kakui & Hiruta 2014; Shoukr *et al*. 1991) or via ballast water (Jones 1991). On the other hand, in the deep-sea, rafting or human transport is unlikely (Blazewicz-Paszkowycz *et al*. 2012).

There are few studies regarding the distribution patterns of Tanaidacea. The most relevant studies are concentrated on a specific geographical region, like the Gulf of Mexico (e.g. Larsen 2005), or to a species or genus specific biogeography (e.g. Bamber 1998; Bamber & Sheader, 2003; Kakui & Angsupanich

2013), or, more-recently, to a species-specific phylogeography (Drumm & Kreiser 2011). Sieg (1986) provided the most comprehensive study of Tanaidacea global distribution patterns. The author mapped the species occurrence and discussed their zoogeographic regions, from Antarctic, Pacific, Atlantic and Indic Ocean. Sieg´s results showed several taxa with both wide horizontal and vertical distributions and suggested further studies to confirm those wide taxa identifications.

Currently, the consensus is that the records of widely distributed species are based on dubious records (Błażewicz-Paszkowycz 2007; Bamber 2010; Larsen *et al.* 2014). Apart from Sieg (1986), several other authors have also discussed this issue and the most controversial point is the species with wide deep-sea distributions. The main reason for this is their known limited dispersal capacity combined with the absence of any possibilities for rafting or human intervention, leading the specialists to believe that many of those records may instead be misidentifications (e.g. Larsen 2005; Błażewicz-Paszkowycz 2007; Larsen *et al*. 2014). Błażewicz-Paszkowycz (2007) considered that the main oceanic currents may be an explanation for the wide distribution of species within one basin (e.g. North/South Atlantic or Circumpolar Antarctic distribution), but the distribution of species in both North Pacific and West Antarctic for instance, is still very questionable.

The traditional classification of Tanaidacea has focused mainly on the morphological comparisons of taxa. However, one of the many difficulties with tanaidacean identification is that several specimens show an extreme morphological similarity (cryptic species). This cryptic nature is often coupled with sexual polymorphism and strong ontogenetic variations (low interspecies variation coupled with high intra-specific variation), thus probably causing many such misidentifications (Larsen *et al*. 2014).

Studies using genetic approaches have tried to shed some light on widely distributed species, suspecting them to be species complex'. An example is *Zeuxo normani* (Richardson, 1905), one of the most widely distributed tanaidaceans which is infamous for harboring species complex'. A recent study revealed a high genetic divergence among specimens collected from the North Atlantic, showing that *Z. normani* harbors at least two new species (Larsen *et al*. 2014; Larsen

2014). Similar results were also found for another widely recorded species, *Tanais dulongii* (Araújo-Silva *et al*. research in progress).

Another important issue regarding tanaidacean distribution patterns is the lack of records from remote areas (e.g. Antarctic, Indian and Pacific Oceans) as well as from regions that for a long time have received very little attention like the Brazilian coast. Considering all the arguments cited above, we believe that the real tanaidacean biodiversity is still underestimated and that the knowledge of their distribution patterns is still very incomplete. Hence, any attempt to provide significant insights for this group, such as new species descriptions, new records, as well as the phylogenetic (molecular and/or morphological) of unstudied, mainly deep-sea taxa, must be considered a necessary complement to the knowledge of tanaidaceans.

1.3. Tanaidacean classification, terminology and general morphology

Tanaidaceans present extensive morphological variety. Their body plan is essentially dorso-ventrally flattened, cylindrical or semi-cylindrical, or rarely discoidal (Figure 1).

Within the peracaridean classification, the tanaidaceans were first placed in the order Amphipoda Latreille, 1816 and then moved to Isopoda Latreille, 1817. Tanaidaceans share with isopods an antennular peduncle (Sieg 1983), but differ from these and many other peracarids by the first two thoracic segments being fused with the cephalon forming a cephalothorax that is dorsally covered by a carapace. Another distinctive feature of the Tanaidacea is that the first pereopods are modified into chelipeds (Figure 2).

After the order Tanaidacea was established, many authors assigned different terminologies for the group (Lang 1953, 1968; Wolff 1956; Gardiner 1975; Sieg 1977; Guţu 1981; Messing 1981; Holdich & Jones 1983; Dojiri & Sieg 1997), but with little consensus to follow a single terminology. Years later, Larsen (2003) finally proposed a standardized anatomical terminology for the four main parts of Tanaidacea: cephalothorax, pereon, pleon and pleotelson, with their respective appendage each (Figure 2).

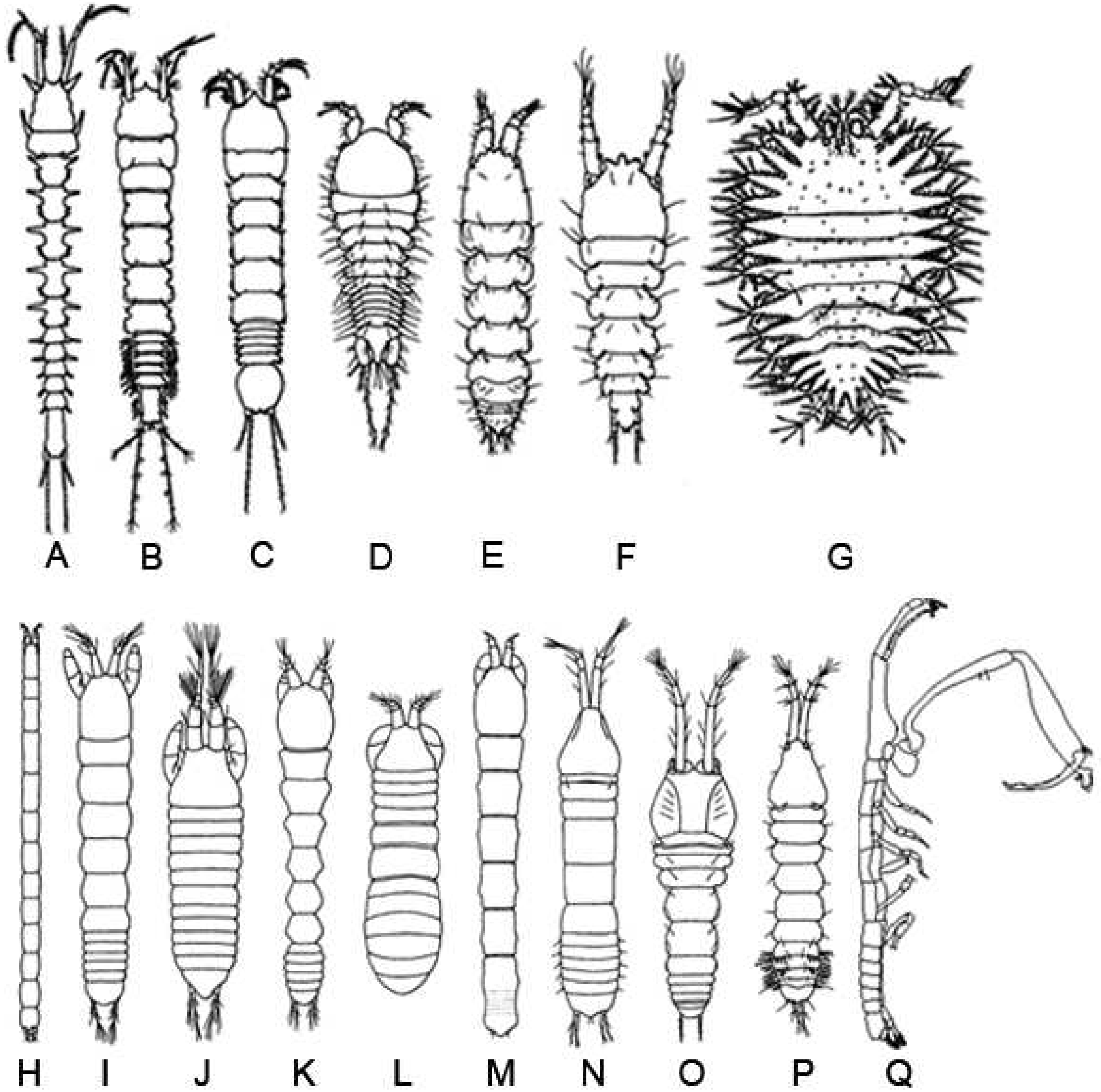


Figure 1. Examples of morphological variation of Tanaidacea. Suborder Apseudomorpha (A-G). Suborders Paratanaidomorpha (H-O), Tanaidomorpha (P) and Neotanaidomorpha (Q). Drawings (A-P) modified from Larsen *et al*. (2015), and (Q) modified from Araújo-Silva *et al*. (2015).

The "cephalothorax" corresponds to the head fused with the two first thoracic segments; two appendages, the maxilliped and the cheliped, arise from these segments. Following the cephalotorax is the "pereon", which corresponds to the first-sixth free thoracic segment named "pereonites"; the appendages belonging to those somites are termed pereopods. The "pleon", is the region formed by the five free abdominal segments (various degrees of fusion occur in the pleon) that are termed as "pleonites"; the corresponding appendages (if any) are termed pleopods. Finally, the "pleotelson" corresponds to the sixth pleonite fused with the telson, which holds appendages named uropods (Figure 2).

The antennule and antenna are attached directly to the head and these appendages are usually equipped with sensory structures such as setae or aesthetascs (Figure 2). Those and similar structures are well discussed in other studies (Guţu & Sieg 1999; Larsen 2003, 2005; Larsen *et al.* 2015). The mouthparts are arranged in anterior-posterior direction: labrum, paired mandibles (left and right), labium, maxillule (or maxilla 1), maxilla (or maxilla 2), maxilliped, and epignath. The mouthparts of the male Neotanaidomorpha and several families of paratanaidomorphans are reduced and non-functional, but they generally retain a maxilliped with short palps (Larsen 2005) (Figure 3).

The chelipeds are attached to the cephalotorax via a coxa, a pseudocoxa, a lateral sclerite, or attached directly to the ventral side of the cephalothorax. Given their great morphological variety, the consensus in standardizing these appendages was particularly important in order to deal with the phylogenetic relationships of tanaidaceans.

1.4. The use of morphological phylogeny on Tanaidacea

Lang (1956) proposed the first tanaidacean systematics and divided the order into two suborders, Monokophora and Dikonophora, mainly based on the number of genital cones on pereonite six. Later, Sieg (1980) proposed a new classification, where the name Monokophora was abandoned and its taxa transferred to a new suborder, Apseudomorpha. The Dikonophora was also abandoned and the taxon split up between two new suborders, Tanaidomorpha and Neotanaidomorpha. Recently, a molecular phylogenic study showed Neotanaidomorpha included in a clade with Tanaidomorpha and was thus demoted to superfamily rank and transferred to Tanaidomorpha (Kakui *et al.* 2011). Therefore, these authors rearranged the systematics scheme with two suborders: Apseudomorpha and Tanaidomorpha (Kakui *et al.* 2011). This arrangement is, however, challenged by the results of this thesis.

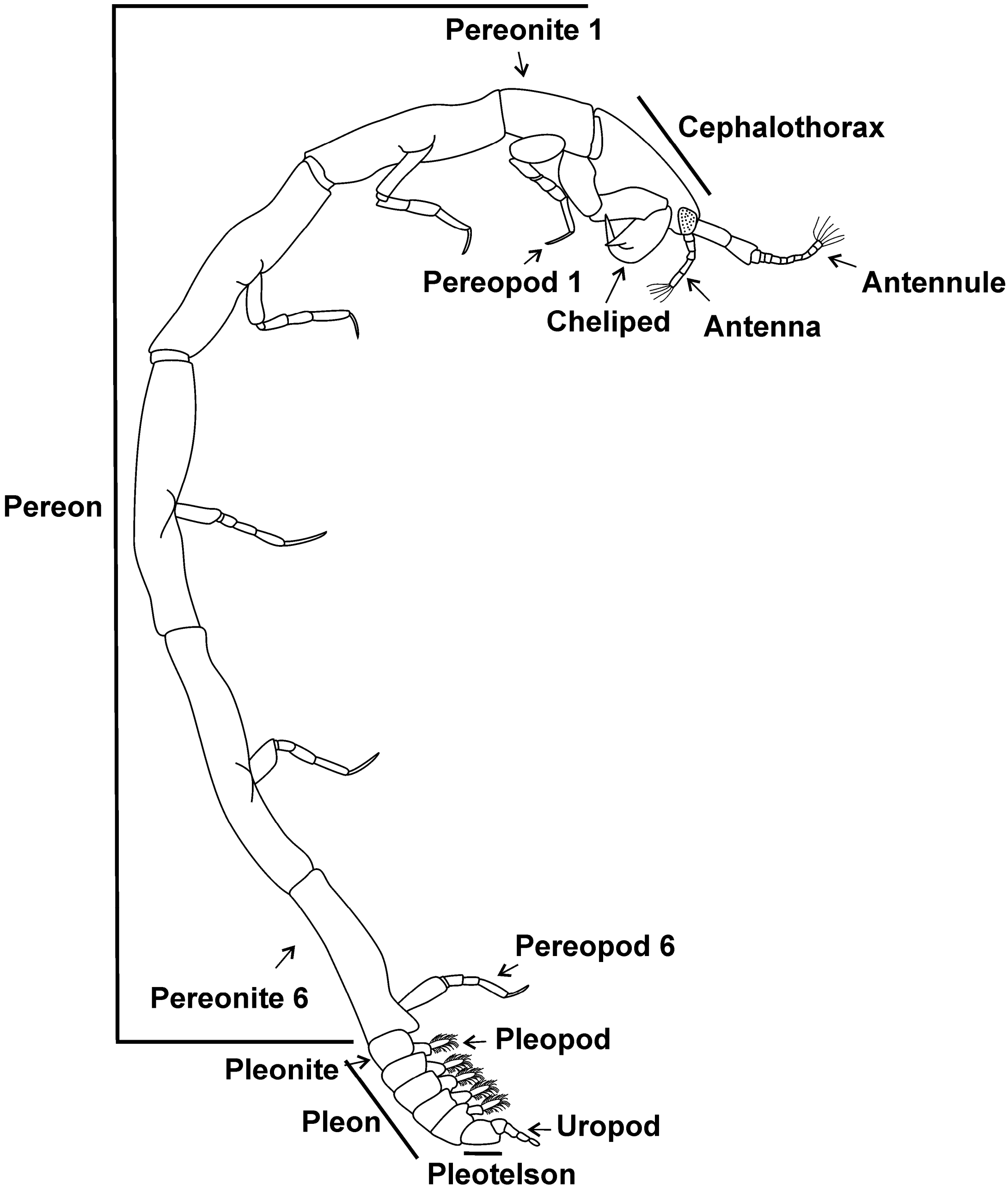


Figure 2. General tanaidacean morphology, body. Drawing modified from Araújo-Silva & Larsen (2012b).

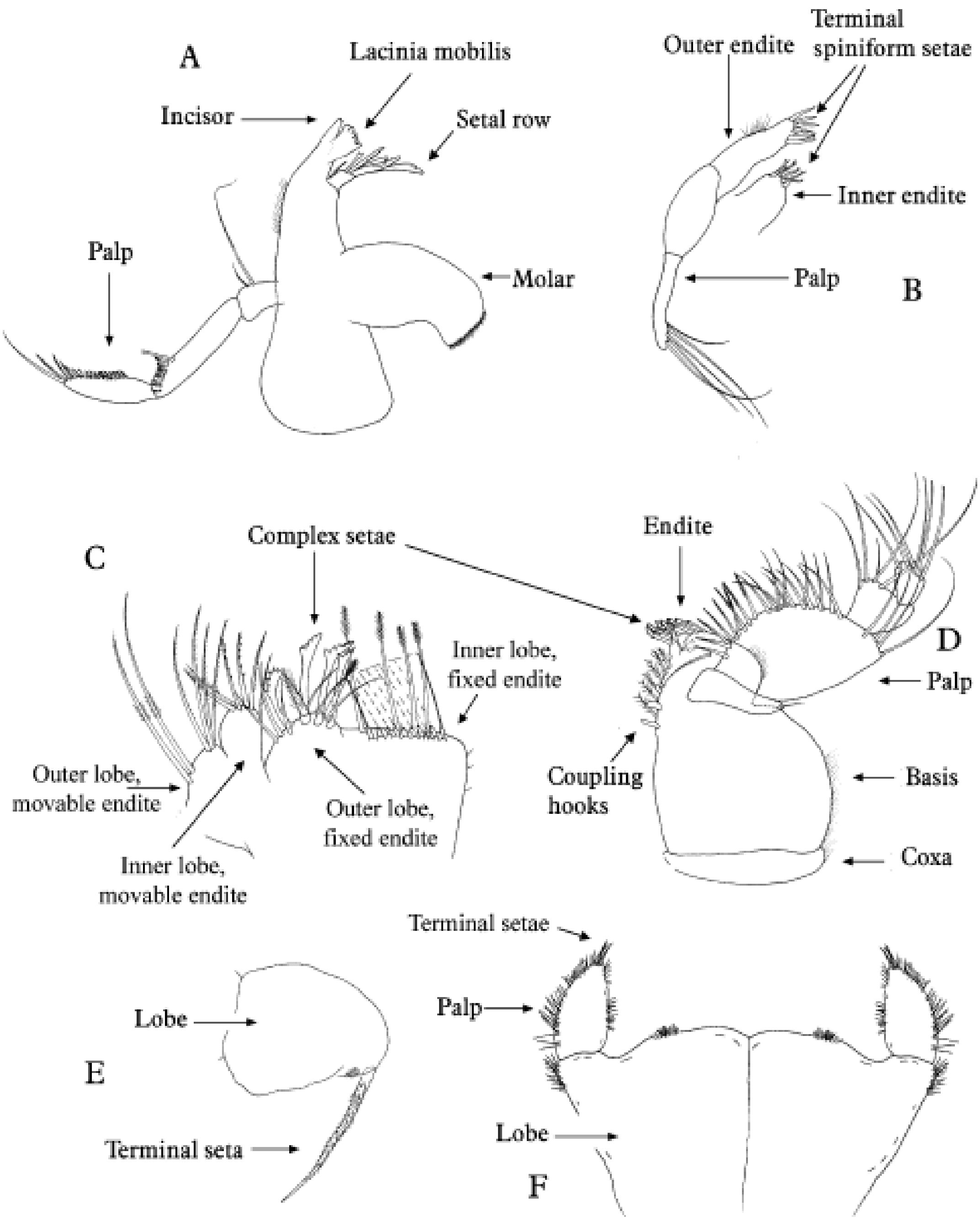


Figure 3. General tanaidacean morphology, mouthparts: (A), mandible; (B), maxillule; (C), maxilla; (D), maxilliped; (E), epignath; (F), labium. Drawings modified from Larsen (2005).

Several morphological phylogenies were performed since the establishment of Tanaidacea (Lang 1956; Sieg 1984), Larsen & Wilson (2002) being the first to introduce computer assisted analyses. Their analyses resulted in a system where several genera were left without family designation (*incertae sedis*). Larsen & Wilson (2002) attributed these results to the many reversals and lack of synapomorphies within the Tanaidacea. Years later, Bird & Larsen (2009) re-did part of Larsen & Wilson (2002) phylogeny including new characters, but surprisingly many other genera were now found as *incertae sedis*, thus resulting in at least one-third of all Paratanaoidea genera being considered as ‘floaters’ within the tanaidaceans systematics. Apart from these studies, other phylogenetic studies have tried to settle the tanaidacean systematics, but most were restricted to a single family (Sieg 1980, 1982; Guerrero-Kommritz & Brandt 2005; Drumm & Heard 2011; Bird 2012; Larsen & Araújo-Silva 2014). For instance, the recently erected family Heterotanoididae Bird, 2012 consisting of species of the genus *Heterotanoides* Sieg, 1977, was previously classified within other families (i.e. Paratanaidae Lang, 1949; Pseudozeuxidae Sieg, 1982; Leptocheliidae Lang, 1973, or even as *incertae sedis* genera). Another example is the family Akanthophoreidae Sieg, 1986, which was first assigned as subfamily Akanthophoreinae within family Anarthruridae Lang, 1971, but this family was shown not to be monophyletic (Larsen & Wilson 2002; Guerrero-Kommritz & Brandt 2005; Bird & Larsen 2009). Recently Błażewicz-Paszkowycz & Bamber (2011) elevated this subfamily to family (i.e. Akanthophoreidae), including the type-genus *Akanthophoreus*, *Chauliopleona* and *Paraleptognathia*, but without a phylogenetic analysis.

All these works suggest that the tanaidacean systematics is still in a state of flux and that to solve its systematics problems, additional research is needed. For instance, by adding more morphological characters (i.e. with new descriptions or re-descriptions) and/or by using molecular approaches.

In order to cast more light on the Tanaidacea systematics, a morphological phylogenetic analysis of the family Akanthophoreidae is presented in the Chapter II of this thesis. This study aims to revise and test the monophyly of Akanthophoreidae, add new characters, and describe new taxa for this family.

1.5. Molecular approaches on Tanaidacea

Over the past decades, several studies based on molecular approaches have provided a valuable supplement to the broader perspective of the taxonomy, biogeography, or population studies of several groups of crustaceans. Those molecular techniques have been extensively used as an important tool to settle still existing uncertainties, especially within the peracaridean systematics. For instance, some of those recent molecular studies have shown that even the position of the order Tanaidacea within Peracarida still remains controversial (Spears *et al*. 2005; Wilson 2009). This is mainly due to a number of previous conflicting morphological and molecular phylogenies that have shown Tanaidacea as sister-taxon to Isopoda (Spears *et al*. 2005), to Cumacea (Poore 2005), or as not monophyletic at all but instead grouping within the Isopoda (Wilson 2009), thus, suggesting that further studies are much needed.

The use of molecular approaches in tanaidacean research is quite recent. The first molecular study was performed by Larsen (2001) who by using a molecular approach identified three cryptic species of the genus *Paratanais* Dana, 1852 from a microhabitat in Australia. Almost a decade later, Drumm (2010) performed the first molecular phylogenetic analyses, for the suborders Apseudomorpha and Tanaidomorpha, using three genes. A year later, Kakui *et al*. (2011) using the ribosomal 18S gene, presented a new classification for Tanaidacea (Figure 4). Other phylogenies were afterwards performed by Kakui *et al*. (2012) and Błażewicz-Paszkowycz *et al*. (2014), but these were restricted to the generic and/or species-specific level. Apart from those phylogenetic studies, other molecular approaches have been used for tanaidaceans. For instance, molecular taxonomy or bar-coding (Larsen *et al.* 2011; Larsen *et al*. 2012; Araújo-Silva *et al*. 2015), genetic divergence (Larsen & Froufe 2013; Larsen *et al.* 2014), population genetics and phylogeography (Drumm & Kreiser 2011).

While there are many difficulties with the tanaidacean morphology (mentioned above), molecular studies are hampered by the fact that successful DNA extraction from tanaidaceans is very difficult. The difficulty in extracting their DNA is caused by the low available starting tissue from smaller specimens (particularly the deep-sea Paratanaidomorpha[1] taxa) and by DNA binding properties of the cuticle. Together, these problems often result in very low DNA yield. Furthermore, the deep-sea collections often reveal many species but only few specimens (termed *singletons*). Unfortunately, those problems were recurrent in the present thesis and frequently the entire animal had to be used. In addition to that, problems in getting successful sequences were also common.

[1] Paratanaidomorpha is here applied in accord with the classification proposed in this thesis (Chapter III, **article 7**).

By all said above, the central aim of the Chapter III is to combine for the first time the molecular and morphological datasets in order to shed some light on the Tanaidacea phylogenetic relationships. In this way, this thesis will also significantly increase the still meager amount of molecular data available for tanaidaceans, especially from deep-sea and *incertae sedis* genera. The molecular dataset is obtained by the combination of partial sequences of three genes: mitochondrial cytochrome *c* oxidase (COI), nuclear Histone 3 (H3) and ribosomal 28S, in order to allow a direct comparison with the only available study that have used more than one gene (i.e. Drumm 2010).

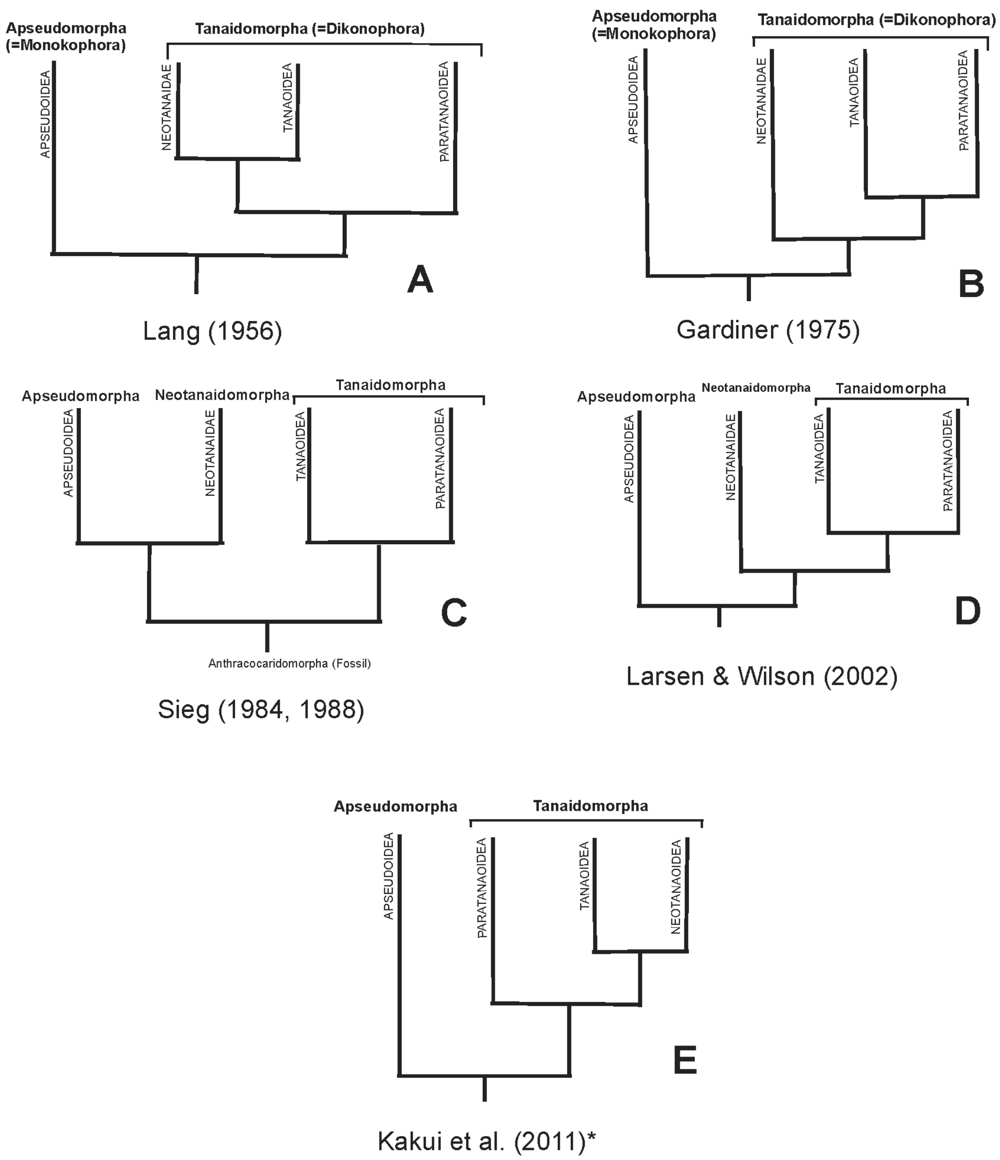


Figure 4. Alternative phylogenetic hypotheses for Tanaidacea suborders. Drawings modified from: (A) Lang (1956); (B) Gardiner (1975); (C) Sieg (1984, 1988); (D) Larsen & Wilson (2002); (E) Kakui *et al.* (2011). *Drawing with asterisk was based on molecular phylogeny only.

1.6. Programs and study area

Over the past decades researchers have suggested that the deep-sea region may be one of the major reservoirs of global biodiversity (Smith 2007). This assumption has become stronger as studies of the deep-sea have shown an impressive number of new species (about 700) in particular areas such as the Antarctic (Southern Ocean) (Brandt *et al*. 2014). Based on that, researchers have speculated that is likely that more species occur in the deep-sea than in any other biome on Earth (Gage & Tyler 1991; Brandt 2012), thus estimating that the number of species that inhabit this area may be approximately 10^5 to 10^8 million species (Grassle & Maciolek 1992).

The deep-sea covers more than 90% of all the entire oceans, but the extreme conditions in this region make exploration much more expensive and difficult than in shallow water (Brandt *et al.* 2004). Contrary to the shallow water, the process of sampling in the deep-sea needs specific sampling tools like, e.g., box-corers, epibenthic sledges, grabs, or multicorers (Figure 5). Due to that, deep-sea expedition activities are often conducted via political incentives to the Economic Exclusive Zones (EEZ), or for oil-companies to have a baseline study for environmental impact assessments. Thus, in a positive way those collections have contributed to characterize, monitor, and most important, extend the distributional records of the marine community fauna in several unexplored areas.

In the present thesis the samples examined were collected from three different Programs:

i) The REVIZEE-NE program (*Programa de Avaliação do Potencial Sustentável dos Recursos Vivos da Zona Econômica e Exclusiva do Brasil*, 1995-2000) was one of the most important sampling campaigns in the northeastern Brazilian waters. This Program aimed to provide an inventory of the living resources in the Exclusive Economic Zone (EEZ) of Brazil, from Continental Shelf to Oceanic Banks (Figure 6). With approximately 8,000 Km, only 43 species of Tanaidacea are formally[2] recorded for Brazilian coast hitherto (Larsen & Araújo-Silva 2009), from which 28 belong to Apseudomorpha, 14 to Tanaidomorpha and one to Neotanaidomorpha. However, these records do not show the real diversity of

[2] Number of species published in peer-reviewed journals until the beginning of this thesis (2012).

tanaidaceans in Brazilian waters, since a great number of specimens from deep and shallow waters are deposited in museums, but still in need of descriptions (personal observation). This suggests that the low diversity in this region is correlated with the lack of specialists.

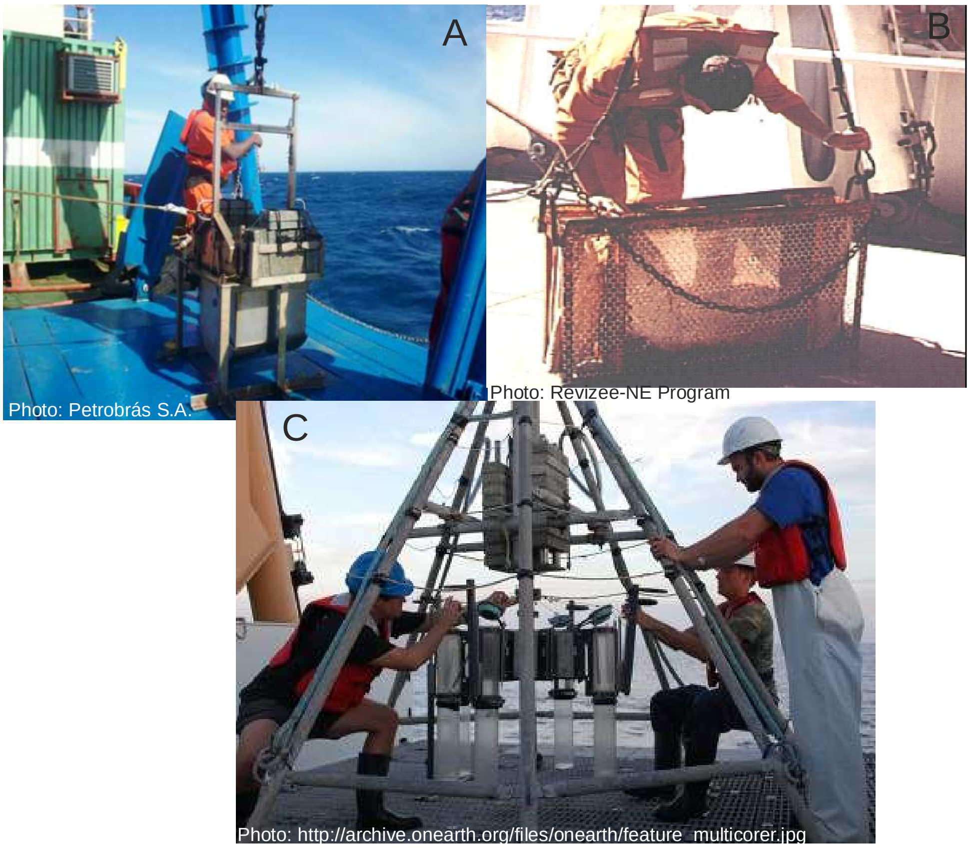


Figure 5. Types of collectors used to sample the material used in this study. (A), Box-corer; (B), dredge; (C), multi-corer.

ii) The ANDEEP I-III program (*ANtarctic benthic DEEP-sea biodiversity*, 2002/2005), aimed to study the influence of the sea-floor habitat diversity on species and genetic diversity, as well as the importance of the Antarctic region as a possible source of data for deep-sea benthic taxa in other oceans (http://www.cedamar.org/en/section1/repository/andeep.html) (Figure 6). The Antarctic Ocean is one of the most remote areas on Earth (Brandt *et al*. 2004). Before the ANDEEP Program, the largest part of the deep-sea in this area was nearly unexplored. Previous records for Tanaidacea from this area were about ten families and 50 species (Sieg 1986; Brandt 1999). Thanks to this Program and other expeditions in the Antarctic, a decade later these numbers have raised to approximately 20 families and 173 species (Brandt *et al*. 2012; Anderson 2013), of which about 13 new species have been already published (Jóźwiak & Błażewicz-Paszkowycz 2007; Larsen *et al*. 2013; Larsen 2013; Larsen & Araújo-Silva 2014). In addition, given the number of specimens deposited in several museums still in need of identification, it is possible that only a small fraction of the present tanaidacean species are yet recorded from the Antarctic slope or abyssal regions (Błazewicz-Paszkowycz *et al*. 2012).

iii) The BIONOD/2012 campaign, aimed to analyze the environmental parameters and the biological living community in the deep-sea area of the Manganese Nodule Province in the Clarion-Clipperton Fracture Zone (MNP-CCFZ), in the Mid-Pacific Ocean (Figure 6). The tanaidaceans of the Pacific are reasonable known, with approximately 250 species recorded (Sieg 1986; Anderson 2013). From the MNP-CCFZ area, about twelve species have been described (Larsen 1999; Larsen 2011a; Larsen 2011b; Wi *et al*. 2014; Araújo-Silva *et al*. 2015).

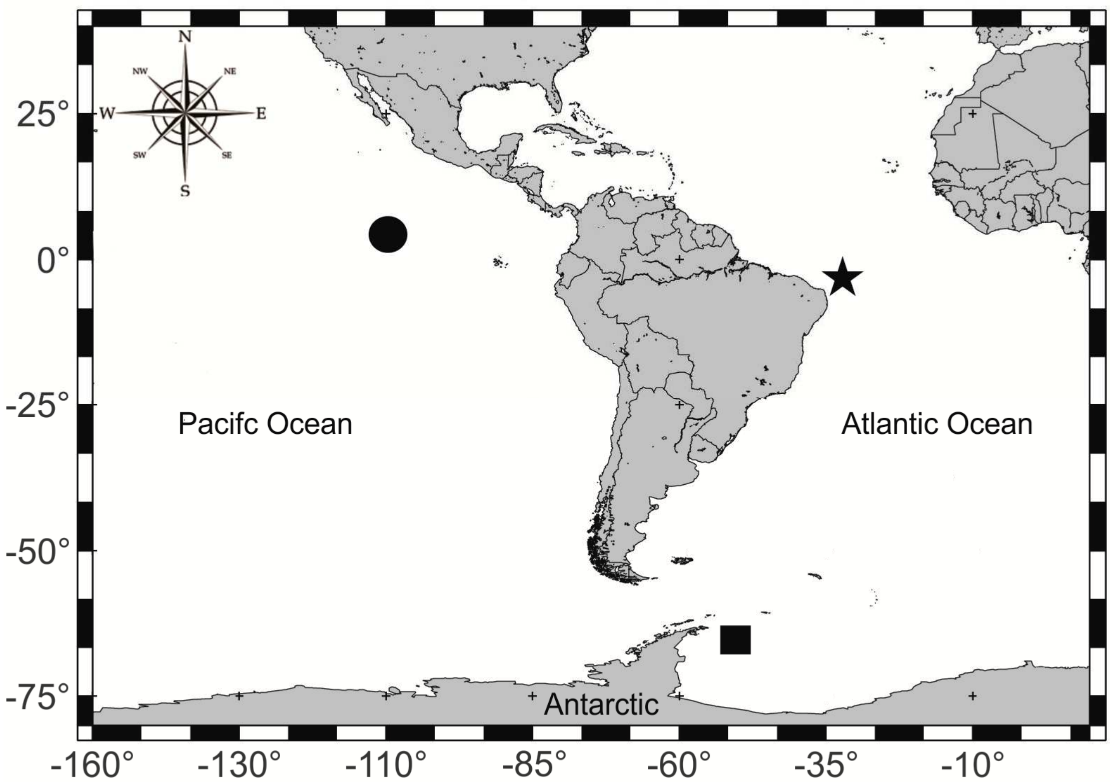


Figure 6. Study areas, marked as: ★Atlantic Ocean (REVIZEE-NE program); ■ Antarctic Ocean (ANDEEP I-III program); ● Pacific Ocean (BIONOD/2012 campaign).

1.7. Objectives

Over the decades, phylogenetic studies of Tanaidacea have indicated that its systematics is still in state of flux, due to the several changes in its systematics. In order to mitigate this issue, studies regarding its morphology as well as molecular approaches are very needed. The central aim of this thesis is to improve the knowledge of Tanaidacea by using both morphological and molecular methods. Also, several issues related to its taxonomy, systematics, morphological and molecular phylogenies are addressed. To reach this main goal we are using as many representative tanaidacean genera from the deep and shallow waters as possible, as well as many *incertae sedis*. These samples were collected during this study, i.e., Pacific Ocean (BIONOD/2012 campaign) and also obtained from deposited collections in Natural History Museum, i.e., Antarctic (ANDEEP I–III program, Natural History Museum, Hamburg) and local museum, Atlantic (REVIZEE-NE program, Museu de Oceanografia Petrônio Alves Coelho/Universidade Federal de Pernambuco).

In order to reach this main objective and elucidate other issues within Tanaidacea, this thesis proposes the following specific objectives:

i) To analyze morphologically the samples collected from shallow water and deep-sea from the Atlantic, Antarctic and Pacific Oceans in order to describe and illustrate the new species to science, as well as to provide new records, whenever possible (**Chapter II**);

ii) To revisit the phylogenetic position of the family Akanthophoreidae, and add new diagnostic characters for this family (**Chapter II**);

iii) To analyze and add morphological characters from the recently described species to a matrix in order to provide a morphological phylogeny for the order Tanaidacea (**Chapter III)**;

iv) To extract DNA and sequence three different genes: mitochondrial cytochrome *c* oxidase (COI), nuclear Histone 3 (H3), and nuclear large subunit ribosomal DNA (28S rRNA), for as many individuals as possible (**Chapter III**);

v) To propose a new comprehensive phylogeny of the order Tanaidacea, combining the morphological and molecular datasets, using as many representative and *incertae sedis* genera as possible (**Chapter III)**.

To address these objectives this thesis is structured through the following chapters:

Chapter I. General Introduction.

Chapter II. Taxonomy, Systematics and Morphological Phylogeny.

Article 1. Araújo-Silva, C.L. & Larsen, K. (2012a). Tanaidacea from Brazil. III. New records and description of a new species collected from REVIZEE-NE Program. *Nauplius*, 20 (2): 87–105.

Article 2. Araújo-Silva, C.L. & Larsen, K. (2012b). Tanaidacea (Tanaidacea: Crustacea) from Brazil. IV. A new genus and two new species from the family Leptocheliidae. *Zootaxa*, 3523: 1–19.

Article 3. Araújo-Silva, C.L., Coelho, P.A.† & Larsen, K. (2013). Tanaidacea (Peracarida) from Brazil. V. Two New Species of *Apseudes* Leach, 1814 from the Northeastern Coast of Brazil. *Crustaceana*, 86 (2) 221–245.

Article 4. Larsen, K. & Araújo-Silva, C.L. (2014a). A new genus of Colletteidae (Crustacea: Peracarida: Tanaidacea) from the Pacific with comments on dimorphic males with species specific characters. *Journal of the Marine Biological Association of the United Kingdom*, 94 (5): 969–974.

Article 5. Araújo-Silva, C.L., Froufe, E. & Larsen, K. (2015). Two new species of family Neotanaidae (Peracarida: Tanaidacea) from the Antarctic and Mid-Pacific Oceans. *Zootaxa*, 4018 (4): 535–552.

Article 6. Larsen, K. & Araújo-Silva, C.L. (2014b). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited III: the family Akanthophoreidae. *Zootaxa*, 3796 (2): 237–264.

Chapter III. Combined Morphological & Molecular Phylogenies

.

Article 7. Araújo-Silva, C.L., Larsen, K. & Froufe, E. (submitted). Tanaidacean (Crustacea: Peracarida) systematics revisited: A combination of morphological and molecular approaches. *Organisms Diversity & Evolution*.

Chapter IV. General Discussion.

1.8. References

Anderson, G. (2013). Tanaidacea-Thirty Years of Scholarship (Vers. 1.0, May, 2013). Available from: http://peracarida.usm.edu/TanaidaceaText.htm (Accessed 14 Sept. 2015).

Araújo-Silva, C.L. & Larsen, K. (2012a). Tanaidacea from Brazil. III. New records and description of a species collected from REVIZEE-NE Program. *Nauplius*, 20 (2): 87–105.

Araújo-Silva, C.L. & Larsen, K. (2012b). Tanaidacea (Tanaidacea: Crustacea) from Brazil. IV. A new genus and two new species from the family Leptocheliidae. *Zootaxa*, 3523: 1–19.

Araújo-Silva, C.L., Froufe, E. & Larsen, K. (2015). Two new species of family Neotanaidae (Peracarida: Tanaidacea) from the Antarctic and Mid-Pacific Oceans. *Zootaxa*, 4018 (4): 535–552.

Bamber, R.N. (1998). Tanaidaceans (Crustacea, Peracarida) from the Southeast of the South China Sea. *Asian Marine Biology*, 15: 169–197.

Bamber, R.N. (2010). In the footsteps of Henrik Nikolaj Krøyer: the rediscovery and redescription of *Leptochelia savignyi* (Krøyer, 1842) sensu stricto (Crustacea: Tanaidacea: Leptocheliidae). *Proceedings of the Biological Society of Washington*, 123 (4): 289–311.

Bamber, R.N., & Bird, G. (1997). *Peracarid crustaceans from Cape d´Aguilar and Hong Kong, III. Tanaidacea: Tanaidomorpha*. Pp. 103–142, *In:* Morton, B. (ed.), The Marine Flora and Fauna of Hong Kong and Southern China IV. Proceedings of the Eighth International Marine Biological Workshop, 2–20 April 1995. Hong Kong, Hong Kong University Press.

Bamber, R.N. & Sheader, M. (2003). *A reinterpretation of the taxonomy and zoogeography of Pakistanapseudes and Swireapseudes (Crustacea: Tanaidacea)*: Hong Kong taxa in the world context. Pp. 167–194, *In:* Morton, B., (ed.), Perspectives on Marine Environment Change in Hong Kong and Southern China, 1977-2001. Proceedings of an International Workshop Reunion Conference, Hong Kong 21-26 October, 2001. Hong Kong, Hong Kong University Press.

Bamber, R., & Sheader, M. (2005). Apseudomorph Tanaidacea (Crustacea: Peracarida) from shallow waters off Sabah, Malaysia. *Systematics and Biodiversity*, 26 (3): 281–303.

Beddard, F.E. (1886). Preliminary notice of the Isopoda collected during the voyage of HMS Challenger. Part III. *Proceedings of the Zoological Society of London*, 26, 97–122.

Bird, G.J. (2012). A new leptochelioid family, Heterotanoididae (Crustacea: Peracarida: Tanaidacea), and a new species of *Heterotanoides* from New Zealand. *Zootaxa*, 3481: 1–26.

Bird, G.J. & Larsen, K. (2009). Tanaidacean phylogeny - the second step: the basal paratanaoidean families (Crustacea: Malacostraca). *Arthropod Systematics and Phylogeny*, 67(2): 137–158.

Błażewicz-Paszkowycz, M. (2007). A revision of the family Typhlotanaidae Sieg 1984 (Crustacea: Tanaidacea) with the remarks on the Nototanaidae Sieg, 1976. *Zootaxa*, 1598: 1–141.

Błażewicz-Paszkowycz, M. & Bamber, R.N. (2011). Tanaidomorph Tanaidacea (Crustacea: Peracarida) from Mud-Volcano and Seep sites on the Norwegian Margin. *Zootaxa*, 3061: 1–35.

Błażewicz-Paszkowycz, M., Bamber, M.R. & Anderson, G. (2012). Diversity of Tanaidacea (Crustacea: Peracarida) in the world's oceans – How far have we come? PLoS ONE 7 (4): e33068. doi:10.1371/journal.pone.0033068.

Błażewicz-Paszkowycz, M., Kobyłecka, E. & Jennings, R.N. (2014). Redescription of wood-associated tanaidacean *Protanais birsteini* (Kudinova-Pasternak, 1970) and its relationship within the Tanaididae. *Deep-Sea Research II*. http://dx.doi.org/10.1016/j.dsr2.2014.10.006

Błażewicz-Paszkowycz, M., Jennings, R.N., Jeskulke, K. & Brix, S. (2014). Discovery of swimming males of Paratanaoidea (Tanaidacea). *Polish Polar Research,* 35 (2): 415–453.

Borowski, C. (2001). Physical disturbed deep-sea macrofauna in the Peru Basin, southeast Pacific, revisited 7 years after the experiment impact. *Deep-Sea Research*, 48: 3809–3839.

Borthagaray, A. I. & Carranza, A. (2007). Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. *Acta Oecologica*, 31: 243–250. http://dx.doi.org/10.1016/j.actao.2006.10.008

Brandt, A. (1999). On the origin and evolution of Antarctic Peracarida (Crustacea, Malacostraca). *Scientia Marina*, 63(1): 261–274.

Brandt, A., De Broyer, C., Ebbe, B., Ellingsen, K.E., Gooday, A.J., Janussen, D., Kaiser, S., Linse, K., Schueller, M., Thomson, M.R.A., Tyler, P.A., & Vanreusel, A. (2012). *Southern Ocean Deep Benthic Biodiversity*. Pp. 291–334, *In:* Rogers, A.D., Johnston, N.M., Murphy, E.J. & Clarke, A. (eds.), Antarctic Ecosystems: An Extreme Environment in a Changing World. Blackwell Publishing Ltd.

Brandt, A., De Broyer, C., Gooday, A.J., Hilbig, B. & Thomson, M.R.A. (2004). Introduction to ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonization history and recent community patterns) — a tribute to Howard L. Sanders. *Deep-Sea Research II*, 51: 1457–1465.

Brandt, A., Griffiths, H., Gutt, J., Linse, K., Schiaparelli, S., Ballerini, T., Danis, B. & Pfannkuche, O. (2014). Challenges of deep-sea biodiversity assessments in the Southern Ocean. *Advances in Polar Science*, 25 (3): 204–212. doi: 10.13679/j.advps.2014.3.00204

Caine, E.A. (1986). Carapace epibionts of nesting Loggerhead sea turtles: Atlantic coast of U.S.A. *Journal of Experimental Marine Biology and Ecology*, 95: 15–26.

Calman, W.T. (1904). XVIII. On the classification of the Crustacea Malacostraca. *The Annals and Magazine of Natural History, Series 7*, 13 (74): 144–158.

Cuvier, M.B. & Valenciennes, M.A. (1835). *Histoire naturelle des poissons.* Tome 10. Chez F.G. Levrault, Paris, xxiv + 482 p.

Dana, J.D. (1849). Conspectus Crustaceorum. Conspectus of the Crustacea of the U.S. Exploring Expedition. *American Journal of Science and Arts, Series 2*, 8: 424–428.

Dana, J.D. (1852). On the classification of the Crustacea Choristopoda or Tetrapoda. *American Journal of Sciences and Arts, Series 2*, 14: 197–306.

Delille, D., Guidi, L.D. & Soyer, J. (1985). *Nutrition of Allotanais hirsutus (Crustacea: Tanaidacea) at Kerguelen Island*. Pages 378–380, *In*: Siegfried, W.R., P.R. Condy, & R.M. Laws (eds.), Antarctic Nutrient Cycles and Food Webs. Springer-Verlag, Berlin.

Desmarest, A.G. (1823). Malacostracés. Pages 138–425, In: Dictionnaire des Sciences Naturelles: Dans Lequel on Traite Méthodiquement des Différens Êtres de la Nature, Considérés Soit en Eux-Mêmes, d´après l´État Actuel de nos Connaissances, Soit Relativement à l´Utilité qu´en Peuvent Retirer la Médecine, l´Agriculture, le Commerce et les Arts; Suivie d´une Biographie des Plus Célèbres Naturalistes, Vol. 28. Strasbourg, Paris.

Dojiri, M. & Sieg, J. (1997). 3. *The Tanaidacea*. Pages 181–278 *In:* Blake, J.A., & P.H. Scott (eds.), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 11. The Crustacea Part 2. The Isopoda, Cumacea and Tanaidacea. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Drumm, D.T. (2003). *Kalliapseudes* (*Mesokalliapseudes*) *macsweenyi* a new species of Kalliapseudidae (Crustacea: Tanaidacea: Apseudomorpha) from mangroves in Florida. *Zootaxa*, 357: 1–12.

Drumm, D.T. (2005). Comparison of feeding mechanisms, respiration, and cleaning behavior in two kalliapseudids, *Kalliapseudes macsweenyi* and *Psammokalliapseudes granulosus* (Peracarida: Tanaidacea). *Journal of Crustacean Biology*, 25 (2): 203–211.

Drumm, D.T. (2010). Phylogenetic relationships of Tanaidacea (Eumalacostraca: Peracarida) inferred from three molecular loci. *Journal of Crustacean Biology*, 30 (4): 692–698.

Drumm, D.T. & Heard, R.W. (2011). Systematic revision of the family Kalliapseudidae (Crustacea: Tanaidacea). *Zootaxa*, 3142: 1–172.

Drumm, D.T. & Kreiser, B. (2011). Population genetic structure and phylogeography of *Mesokalliapseudes macsweenyi* (Crustacea: Tanaidacea) in the northwestern Atlantic and Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*. doi:10.1016/j.jembe.2011.10.023.

Gardiner, L.F. (1975). The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea). *Smithsonian Contributions to Zoology*, 170: 1–265.

Gage, J.D. & Tyler, P.A. (1991). *Deep-Sea Biology*. A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press, Cambridge.

Gamô, S. (1984). A new remarkably giant tanaid, *Gigantapseudes maximus* sp. nov. (Crustacea) from the abyssal depths far off southeast of Mindanao, the Philippines. *Science Reports of the Yokohama National University, Section II Biology and Geology*, Nº. 31, pp. 1–12.

Gnewuch, T. & Crokerr, A. (1985) Macroinfauna of northern New England marine sand. The biology of *Mancocuma stellifera* Zimmer, 1943 (Crustacea, Cumacea). *Canadian Journal of Zoology*, 51:1011–1020.

Grassle, J. F. & Maciolek, N.J. (1992). Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *The American Naturalist*, 139 (2): 313–341.

Guerrero-Kommritz, J. & Brandt, A. (2005). Phylogenetic analysis of genera of 'Akanthophoreinae' (Crustacea: Tanaidacea). *Organisms, Diversity & Evolution*, 5 (4): 285–296.

Guţu, M. (1981). A new contribution to the systematics and phylogeny of the suborder Monokonophora (Crustacea, Tanaidacea). *Travaux du Muséum National d´Histoire Naturelle "Grigore Antipa"* 23: 81–108.

Guţu, M. & Iliffe, T.M. (1985). The redescription of *Apseudes* (?) *propinquus* Richardson, 1902 (Crustacea, Tanaidacea) from Bermuda Caves. *Travaux du Muséum National d´Histoire naturelle "Grigore Antipa*" 27: 55–62.

Guţu, M. & Sieg, J. (1999). 9 *Ordre des Tanaïdacés* (Tanaidacea Hansen, 1895). Pages 353–389, *In:* Forest, J., M. Bacescu, D. Bellan-Santini, G.A. Boxshall, Ph. Cals, J.-P. Casanova, H. Dalens, M. Guţu, R.R. Hessler, J.P. Lagardère, Th. Monod, H. Nouvel, I. Petrescu, M.-L. Roman, J. Sieg, J.-P. Trilles, & L. Watling, L. (eds.), Traité de Zoologie: Anatomie, Systématique, Biologie, 7, Crustacés, 3A. Péracarides [Treatise on Zoology: Anatomy, Systematics, Biology, 7, Crustaceans, 3A. Peracarida]. Mémoires de l´Institut Océanographique, Monaco, 19. Musée Océanographique de Monaco, Monaco.

Hassack, E. & Holdich, D.M. (1987). The tubiculous habit amongst the Tanaidacea (Crustacea, Peracarida) with particular reference to deep-sea species. *Zoologica Scripta*, 16: 223–233.

Highsmith, R.C. (1983). Sex reversal and fighting behavior: coevolved phenomena in a tanaid crustacean. *Ecology*, 64: 719–726.

Holdich, D.M. & Jones, J.A. (1983). The distribution and ecology of British shallow-water tanaid crustaceans (Peracarida, Tanaidacea). *Journal of Natural History*, 17 (2): 157–183.

Jones, M.M. (1991). Marine organisms transported in ballast water. A review of the Australian scientific position. *Bureau of Rural Resources Bulletin*, 11: 1–45.

Jóźwiak, P. & Błażewicz-Paszkowycz, M. (2007). Apseudomorpha (Malacostraca: Tanaidacea) of the ANDEEP III Antarctic Expedition. *Zootaxa*, 1610: 1–25.

Kakui, K. & Angsupanich, S. (2013). Description of three species of *Halmyrapseudes* (Crustacea: Tanaidacea: Parapseudidae), with a discussion of biogeography. *Zootaxa*, 3736 (4): 345–367.

Kakui, K. & Hiruta, C. (2014). Diverse Pereopodal Secretory Systems Implicated in Thread Production in an Apseudomorph Tanaidacean Crustacean. *Journal of Morphology*, 275: 1041–1052.

Kakui, K., Katoh, T., Hiruta, S.F., Kobayashi, N. & Kajihara, H. (2011). Molecular systematics of Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of suborder/superfamily-level classification. *Zoological Science*, 28: 749–757.

Kakui, K., Kobayashi, N. & Kajihara, H. (2012). Phylogenetic position of *Arctotanais* in the suborder Tanaidomorpha (Peracarida: Tanaidacea). *Journal of Crustacean Biology*, 32 (1): 127–139.

Klitgaard, A.B. (1995). The fauna associated with outer shelf and upper slope sponges (Porifera, Demospongiae) at the Faroe Islands, Northeastern Atlantic. *Sarsia*, 80:1–22.

Lang, K. (1949). Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologie, Series 1*, 42 (18): 1–14.

Lang, K. (1953). *Apseudes hermaphroditicus* n.sp. A hermaphroditic Tanaide from the Antarctic. *Arkiv för Zoologi, Series 2,* 4: 341–350 (plates I-IV).

Lang, K. (1956). Neotanaidae nov. fam., with some remarks on the phylogeny of the Tanaidacea. *Arkiv för Zoologi*, 9: 469–475.

Lang, K. (1968). *Deep-Sea Tanaidacea*. Pp. 23–210, *In:* Galathea Report, Vol. 9. Danish Science Press, Copenhagen.

Lang, K. (1971). Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen. 6. Revision der Gattung *Paranarthrura* Hansen, 1913, und Aufstellung von zwei neuen Familien, vier neuen Gattungen und zwei neuen Arten. *Arkiv för Zoologi, Series 2*, 23: 361–401.

Lang, K. 1973. Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen (Crustacea). 8. Die Gattungen *Leptochelia* Dana, *Paratanais* Dana, *Heterotanais* G.O. Sars und *Nototanais* Richardson. Dazu einige Bemerkungen über die Monokonophora und ein Nachtrag. *Zoologica Scripta*, 2: 197–229.

Larsen, K. (1999). Pacific Tanaidacea (Crustacea): Revision of the genus *Agathotanais*, with description of three new species. *Records of the Australian Museum*, 51: 99–112.

Larsen, K. (2001). Morphological and molecular investigation of polymorphism and cryptic species in tanaid crustaceans: implications for tanaid systematics and biodiversity estimates. *Zoological Journal of the Linnean Society,* 131: 353–379.

Larsen, K. (2003). Proposed new standardized anatomical terminology for the Tanaidacea (Peracarida). *Journal of Crustacean Biology*, 23: 644–661.

Larsen, K. (2005). *Deep-Sea Tanaidacea (Peracarida) from the Gulf of Mexico*. Pp. 391. Brill, Leiden.

Larsen, K. (2006). Tanaidacea (Crustacea; Peracarida) from chemically reduced habitats - the hydrothermal vent system of the Juan de Fuca Ridge, Escabana Trough and Gorda Ridge, Northeast Pacific. *Zootaxa*, 1164: 1–33.

Larsen, K. (2011a). Tanaidaceans (Crustacea) from the Central Pacific Manganese Nodule Province. I. The genera *Collettea*, *Robustochelia* and *Tumidochelia*. *ZooKeys*, 87:19–41.

Larsen, K. (2011b). The tanaidacean assemblage from the Central Pacific Manganese Nodule Province. II. The genera *Stenotanais* and *Typhlotanais* (Crustacea). *Zootaxa*, 3088: 39–53.

Larsen, K. (2013). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited II: the family Anarthruridae and family *incertae sedis*, with descriptions of three new species and the erection of a new genus. *Zootaxa*, 3694 (4): 367–380.

Larsen, K. (2014). New species of the genus *Zeuxo* (Peracarida, Tanaidacea). *Crustaceana*, 87 (6): 715–754.

Larsen, K., Araújo-Silva, C.L. & Coelho, P.A. (2009). Tanaidacea from Brazil. I. The family Tanaellidae Larsen & Wilson, 2002. *Zootaxa*, 2141: 1–19.

Larsen, K. & Araújo-Silva, C.L. (2014). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited III: the family Akanthophoreidae. *Zootaxa*, 3796 (2): 237–264.

Larsen, K. & Froufe, E. (2013). A new polymorphic species of *Leptochelia* (Crustacea: Tanaidacea) from Guinea Bissau, West Africa, with comments on genetic variation within *Leptochelia*. *African Invertebrates*, 54 (1): 105–125.

Larsen, K. & Hansknecht, T. (2004). A new genus and species of freshwater tanaidacean, *Pseudohalmyrapseudes aquadulcis* (Apseudomorpha: Parapseudidae), from Northern Territory, Australia. *Journal of Crustacean Biology*, 24 (4): 567–575.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny, the first step: The superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research*, 40 (4): 205–222.

Larsen, K., Bertocci, I. & Froufe, E. (2011). *Apseudes talpa* revisited (Crustacea; Tanaidacea). The impact on apseudidaen systematics. *Zootaxa*, 2886: 19–30.

Larsen, K., Nagaoka, R. & Froufe, E. (2012). Tanaidacea (Crustacea) from Macaronesia III. The shallow-water Tanaidomorpha from the Cape Verde archipelago. *Zootaxa*, 3498: 24–44.

Larsen, K., Błażewicz-Paszkowycz, M. & Cunha, M.R. (2006). Tanaidacean (Crustacea: Peracarida) fauna from chemically reduced habitats - the lucky strike hydrothermal vent system, mid-atlantic ridge. *Zootaxa*, 1187: 1–36.

Larsen, K., Bird, G. & Ota, M. (2013). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited I: the family Agathotanaidae Lang, with description of four new species. *Zootaxa*, 3630 (3): 424–444.

Larsen, K., Tuya, F. & Froufe, E. (2014). Genetic divergence of tanaidaceans (Crustacea: Peracarida) with low dispersal ability. *Scientia Marina*, 78 (1): 81–90.

Larsen, K., Guţu, M. & Sieg, J. (†) (2015). Chapter 59. *Order Tanaidacea* Dana, 1849. Crustacea 5 (59): 249–328. Leiden.

Latreille, P.A. (1816). Cephus. *Nouveau Dictionnaire d'Histoire Naturelle*, 5: 497-498

Latreille, P.A. (1817). *Les crustaces, les arachnides et les insects*. Vol. 3. *In:* Cuvier, G. Le Regne Animal, distribue d'apres son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparee. Deterville, Paris. 653 pp.

Mañé-Garzón, F. (1949). Un neuvo tanaidáceo ciego de Sud América, *Kalliapseudes schubartii*, nov. sp. *Comunicaciones Zoológicas del Museo del Museo de Historia Natural de Montevideo 3*, (52): 1–6.

Martin, J.W. & Davis, G.E. (2001). An updated classification of the Recent Crustacea. *Natural History Museum of Los Angeles County Science Series*, 39: 1–124.

Messing, C.G. (1981). Notes on recent changes in tanaidacean terminology. *Crustaceana*, 41 (1): 96–101.

Messing, C.G. (1983). Postmarsupial development and growth of *Pagurapseudes largoensis* McSweeny (Crustacea, Tanaidacea). *Journal of Crustacean Biology*, 3: 380–408.

Rathbun, M. J. (1986). The genus *Callinectes*. P.U.S. Mus. xviii, pp. 349–375, pls. xii-xxviii.

Montagnolli, W., Zamboni, A., Luvizotto-Santos, R. & Yunes, J.S. (2004). Acute effects of *Microcystis aeruginosa* from the Patos Lagoon Estuary, southern Brazil, on the microcrustacean *Kalliapseudes schubartii* (Crustacea: Tanaidacea). *Archives of Environmental Contamination and Toxicology*, 46 (4): 463–469.

Morales-Vela, B., Suárez-Morales, E., Padilla-Saldívar, J. & Heard, R.W. (2008). The tanaid *Hexapleomera robusta* (Crustacea: Peracarida) from the

Caribbean manatee, with comments on other crustacean epibionts. *Journal of the Marine Biological Association of the United Kingdom*, 88 (3): 591–596.

Oliver, J.S. & Slattery, P.N. (1985). Effects of crustacean predators on species composition and population structure of soft-bodied infauna from McMurdo Sound, Antarctica. *Ophelia*, 24 (3): 155–175.

Pérez Farfante, I. (1967). A new species and two new subspecies of shrimp of the genus *Penaeus* from the Western Atlantic. *Proceedings of the Biological Society of Washington*, 80: 83–100.

Poore, G.C.B. (2005). Peracarida: monophyly, relationships and evolutionary success. *Nauplius*, 1 (3): 1–27.

Richardson, H. (1905). Descriptions of a new genus of Isopoda belonging to the family Tanaidæ and of a new species of *Tanais*, both from Monterey Bay, California. *Proceedings of the United States National Museum*, 28 (1400): 367–370.

Rumbold, C.E., Obenat, S.M., Leonardi, M. S. & Spivak, E. D. (2015). Intersex in the gonochoristic crustacean *Tanais dulongii* (Audouin, 1826) (Peracarida: Tanaidacea: Tanaididae): a comparison of external reproductive characteristics, *Journal of Natural History*. DOI: 10.1080/00222933.2014.981309

Saigusa, M. & Oishi, K. (2000). Emergence Rhythms of Subtidal Small Invertebrates in the Subtropical Sea: Nocturnal Patterns and Variety in the Synchrony with Tidal and Lunar Cycles. *Zoological Science*, 17: 241–251.

Sars, G.O. (1882). Revision af gruppen: Isopoda Chelifera med charakteristik af nye herhen hørende arter og slægter. *Archiv for Mathematik og Naturvidenskab*, 7: 1–54 (Norwegian and Latin).

Schram, F.R., Sieg, J. & Malzahn, E. (1986). Fossil Tanaidacea. *Transactions of the San Diego Society of Natural History*, 21 (8): 127–144.

Shoukr, F.A., Mona, M.H. & El-Sheikh, H. (1991). Identification of marine fouling Crustacea in the Suez Canal, with a note on distribution and migration. *Pakistan Journal of Zoology*, 23: 79–83.

Sieg, J. (1977). Taxonomische Monographie der familie Pseudotanaidae (Crustacea, Tanaidacea). *Mitteilungen aus dem Zoologischen Museum in Berlin*, 53: 1–109.

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzieger*, 205 (5-6): 401–416.

Sieg, J. (1982). Über ein "connecting link" in der Phylogenie der Tanaidomorpha (Tanaidacea). *Crustaceana*, 43 (1): 65–77.

Sieg, J. (1983). *Evolution of Tanaidacea*. Pp. 229–256. *In:* Schram, F.R. (ed.), Crustacean Phylogeny. A.A. Balkema, Rotterdam, The Netherlands.

Sieg, J. (1984). Fact documentation and literature database for the crustacean order Tanaidacea. *Systematics Association*, Special Volume 26: 125–136.

Sieg, J. (1986). *Distribution of the Tanaidacea: Synopsis of the known data and suggestions on possible distribution patterns*. Pp. 165–194, *In:* Gore, R.H. & Heck, K.L. (eds.), Crustacean Biogeography, Crustacean Issues 4. A.A. Balkema, Rotterdam, The Netherlands.

Sieg, J. (1988). Das phylogenetische System der Tanaidacea und die Frage nach Alter und Herkunft der Crustaceenfauna des antarktischen Festlandsockels [The phylogenetic system of the Tanaidacea and the question of age and origin of the crustacean fauna on the Antarctic shelf]. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, 26: 363–379.

Sieg, J. & Heard, R.W. (1985). Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico. IV. On *Nototanoides trifurcatus* gen. nov., sp. nov., with a key to the genera of the Nototanaidae. *Gulf Research Reports*, 8 (1): 51–62.

Sieg, J. & Zibrowius, H. (1988). Association of the tube inhabiting tanaidacean, *Bifida scleractinicola* gen. nov., sp. nov., with bathyal scleractinians off New Caledonia (Crustacea Tanaidacea - Cnidaria Scleractinia). *Mésogée*, 48: 189–199.

Smith, C.R., Paterson, G., Lambshead, J., Glover, A., Rogers, A., Gooday, A., Kitazato, H., Sibuet, M., Galéron, J. & Menot, L. (2007). Biodiversity, species ranges, and gene flow in the abyssal Pacific nodule province: predicting and managing the impacts of deep seabed mining. Pp 1–45.

Report compiled for the International Seabed Authority, II. Series, ISBN: 978-976-95217-2-8.

Sokolova, M.N. (1972). Trophic structure of deep-sea macrobenthos. *Marine Biology*, Berlin, 16: 1–12.

Spaccesi, F.G. & Rodrigues Capítulo, A. (2012). Benthic communities on hard substrates covered by *Limnoperna fortunei* Dunker (Bivalvia, Mytilidae) at an estuarine beach (Río de la Plata, Argentina). *Journal of Limnology*, 71 (1): 144–153. DOI: 10.4081/jlimnol.2012.e15

Spears, T., DeBry, R.W., Abele, L.G. & Chodyla, K. (2005). Peracarid monophyly and interordinal phylogeny inferred from nuclear small- subunit robosomal DNA sequences (Crustacea: Malacostraca: Peracarida). *Proceedings of the Biological Society of Washington,* 118 (1): 117–157.

Suárez-Morales, Londoño-Mesa, E.M., & Heard, R.W. (2011). Discovery of a new genus of tanaidacean (Crustacea: Tanaidacea: Mirandotanaidae) found associated with a deep-sea terebellid polychaete. *Contributions to Zoology*, 80 (2): 157–167.

Thurston, M.H., Billett, D.S.M. & Hassack, E. (1987). An association between *Exspina typica* Lang (Tanaidacea) and deep-sea holothurians. *Journal of the Marine Biological Association of the United Kingdom*, 67: 11–15.

Wang, C.F., Ren, X.Q. & Xu, R.L. (2010). Composition, Abundance, and Diversity of the Peracarida on Different Vegetation Types in the Qi'ao-Dan'gan Island Mangrove Nature Reserve on Qi'ao Island in the Pearl River Estuary, China. *Zoological Studies*, 49 (5): 608–615.

Wi, J.H., Suh, H.L. & Yu, O.H. (2014). Two new species of the deep-sea genus *Neotanais* Beddard, 1886 (Tanaidacea: Neotanaididae) from the Eastern Central Pacific. *Journal of Crustacean Biology*, 34(6): 875–885.

Wilson, G.D.F. (2009). The phylogenetic position of the Isopoda in the Peracarida (Crustacea: Malacostraca). *Arthropod Systematics and Phylogeny*, 67 (2): 159–198.

Wolff, T. (1956). *Crustacea Tanaidacea from depths exceeding 6000 meters*. Pp. 187–241, *In:* Bruun, A., Greve, S., Spärck, R. & Wolff, T. (eds.), Galathea Report: Scientific Results of the Danish Deep-Sea Expedition Round the World 1950–52, Vol. 2. Danish Science Press, Copenhagen.

Wolff, T., *et al.* (1977). Hadal life as analyzed from photographs. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 139: 263–336.

WoRMS (World Register of Marine Species). (2015). WoRMS taxon details. Available from: http://www.marinespecies.org/index.php (accessed 15 December 2015)

CHAPTER II. TAXONOMY, SYSTEMATICS AND MORPHOLOGICAL PHYLOGENY

Article 1. Araújo-Silva, C.L. & Larsen, K. (2012a). Tanaidacea from Brazil. III. New records and description of a new species collected from REVIZEE-NE Program. *Nauplius*, 20 (2): 87–105.

Article 2. Araújo-Silva, C.L. & Larsen, K. (2012b). Tanaidacea (Tanaidacea: Crustacea) from Brazil. IV. A new genus and two new species from the family Leptocheliidae. *Zootaxa*, 3523: 1–19.

Article 3. Araújo-Silva, C.L., Coelho, P.A.† & Larsen, K. (2013). Tanaidacea (Peracarida) from Brazil. V. Two New Species of *Apseudes* Leach, 1814 from the Northeastern Coast of Brazil. *Crustaceana*, 86 (2) 221–245.

Article 4. Larsen, K. & Araújo-Silva, C.L. (2014a). A new genus of Colletteidae (Crustacea: Peracarida: Tanaidacea) from the Pacific with comments on dimorphic males with species specific characters. *Journal of the Marine Biological Association of the United Kingdom*, 94 (5): 969–974.

Article 5. Araújo-Silva, C.L., Froufe, E. & Larsen, K. (2015). Two new species of family Neotanaidae (Peracarida: Tanaidacea) from the Antarctic and Mid-Pacific Oceans. *Zootaxa*, 4018 (4): 535–552.

Article 6. Larsen, K. & Araújo-Silva, C.L. (2014b). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited III: the family Akanthophoreidae. *Zootaxa*, 3796 (2): 237–264.

Nauplius, 20 (2): 87–105 (2012)

Article 1. Tanaidacea from Brazil. III. New records and description of a new species collected from REVIZEE-NE Program

Catarina L. Araújo-Silva & Kim Larsen

(CLAS, KL) Laboratory for Marine Community Ecology and Evolution, CIIMAR (Centro Interdisciplinar de Investigação Marinha e Ambiental), University of Porto, Rua dos Bragas, 289, 4050-123 Porto, Portugal (present address). Capes Foundation, Ministry of Education of Brazil, Brasília-DF, 70040-020, Brazil. E-mails: (CLAS) katelas@hotmail.com (corresponding author); (KL) tanaids@hotmail.com

Abstract

A new species of *Paratanais* Dana, 1852, *Paratanais coelhoi* n. sp., is described and new records for *Paradoxapseudes intermedius* (Hansen, 1895), *Intermedichelia gracilis* Guţu, 1996, *Vestigiramus* sp., *Nototanoides* cf. *trifurcatus* Sieg & Heard, 1985, *Biarticulata* sp. and *Arhaphuroides* sp. are provided from northeastern Brazil based on collections from the REVIZEE-NE Program. This raises the number of tanaidacean species from the Brazilian coast from 45 to 49. *Paratanais coelhoi* n. sp. shares morphological features such as habitus shape, maxilliped palp setation, and cheliped proportions with *P. oculatus* (Vanhöffen, 1914), *P. martinsi* Bamber & Costa, 2009, *P. tara* Bird, 2011 and *P. euelpis* Barnard, 1920. The new species can, however, be distinguished by a unique combination of characters including: pleonites 1–4 with lateral circumplumose setae while the 5th with simple seta only; antennule article 1 stout; cheliped propodus with one specialized outer ‘S’-shaped broad seta; pereopod 1 merus length with 1.7 times as long as wide; pereopod 2 merus without ventral spiniform seta; uropodal endopod biarticulate, exopod uniarticulate as well as other characters.

Key words: northeastern Brazil, Peracarida, Paratanaidae, *Paratanais*, Tanaidacean.

Introduction

While quite a number of taxonomic papers on the Tanaidacea of Brazil have been published (Krøyer 1842; Mañé-Garzón 1949; Lang 1956; Silva-Brum 1969, 1971, 1973, 1974, 1978; Băcescu 1979, 1984, 1986; Masunari & Sieg 1980; Sieg 1983; Băcescu & Absalão 1985; Guţu 1996, 1998; Larsen 1999; Santos & Pires-Vanin 2006; Santos 2007; Santos & Hansknecht 2007; Larsen *et al*. 2009; Araújo-Silva & Larsen 2012; Santos *et al*. 2012), most of species are described from southeastern Brazilian waters or deep-sea habitats. Among 45 species recorded from Brazil, only eleven were published from northeastern coast (Guţu 1998; Araújo-Silva & Larsen 2012): *Intermedichelia jesseri* Araújo-Silva & Larsen, 2012, *Leptochelia dubia* (Krøyer, 1842), *L. forresti* (Stebbing, 1896), *Makraleptochelia potiguara* Araújo-Silva & Larsen, 2012, *Neotanais tricarinatus* Gardiner, 1975, *Parapagurapseudopsis carinatus* Silva-Brum, 1973, *Parapseudes inermis* (Silva-Brum, 1973), *Paratanais oculatus* (Vanhöffen, 1914), *Psammokalliapseudes granulosus* Silva-Brum, 1973, *Saltipedis* (*Saltipedis*) *paulensis* (Silva-Brum, 1971) and *Zeuxo* (*Parazeuxo*) *coralensis* Sieg, 1980a. It is unlikely that so little tanaidacean diversity is present in this area, since the northeastern coast represents at least one-third of the entire Brazilian coast. Moreover, tropical environments usually display higher biodiversity than at higher latitudes (Rapoport 1982), suggesting that the lack of records, are more likely correlated to sampling effort.

At the end of the twentieth century (1995–2000) the REVIZEE Program (Programa de Avaliação do Potencial Sustentável dos Recursos Vivos da Zona Econômica e Exclusiva do Brasil), a survey of the fauna and flora of the exclusive economic zone of the coast of Brazil, was conducted. During this program, collections were made on northeastern coast (NE Score) along the continental shelf and oceanic banks of the Archipelago of Fernando de Noronha and North Chain Banks of Brazil. These collections revealed a number of members of several of tanaidacean families, including the Apseudidae Leach, 1814; Leptocheliidae Lang, 1973; Leptognathiidae Sieg, 1976; Metapseudidae Lang, 1970; Nototanaidae Sieg, 1976; Paratanaidae Lang, 1949 and Tanaellidae Larsen & Wilson, 2002.

The family Paratanaidae currently contains five genera and occurs in both deep (*Bathytanais* Beddard, 1886 and *Pseudobathytanais* Kudinova-Pasternak, 1990) and shallow waters (*Bathytanais*; *Paratanais* Dana, 1852; *Triparatanais* Bamber & Chatterjee, 2010; *Xeplenois* Bamber, 2005), but the majority of species are from shallow water. Bird & Larsen (2009) regarded Paratanaidae as one of the few monophyletic families that has remained stable since its establishment and probably the only one that is not controversial. The genus *Teleotanais* Lang, 1956 was assigned by Bamber (2008) to a new subfamily principally on the basis of 1–4 circumplumose epimeral pleonal setae; however, this genus is unlike any paratanaid and appears more leptocheliid-like, and it was raised to family-level by Bird & Larsen (2009).

The main diagnostic characters of the family Paratanaidae are the presence of maxilliped endites laterally expanded and wider than basis; pereopod 4–6 carpus with clinging apparatus present as strong spiniform setae and scales (complex or not) but without microtrichial field; pleonites 1–5 (or 1–4) with lateral circumplumose setae (Bird & Larsen 2009: 155), as well as other characters. Even though these characters seem to be consistent, Sieg (1986: 57) stated that the systematics of the genus *Paratanais* is quite confusing, and that a revision was required. Such a revision is currently under way (G.J. Bird, pers. comm.).

The genus *Paratanais* is represented on the Brazilian coast by *P. oculatus* and was first recorded by Silva-Brum (1973: 4–5) from Bahia (northeastern Brazil) but this identification is uncertain (see remarks of *P. coelhoi* n. sp.). In this study, a new species of *Paratanais* is described and new records are provided for *Nototanoides* cf. *trifurcatus* Sieg & Heard, 1985, *Biarticulata* sp., *Arhaphuroides* sp., *Paradoxapseudes intermedius* (Hansen, 1895), *Intermedichelia gracilis* Guţu, 1996 and *Vestigiramus* sp., thus increasing the number of tanaidacean species known from the Brazilian coast from 45 to 49. This is the third study on the systematics of the Tanaidacea from Brazil and the first of a series of papers based on the REVIZEE-NE Program collection from the northeastern part of Brazil.

Material and Methods

Specimens were collected from the continental shelf between the mouth of Parnaíba River (Piauí state) and Salvador (Bahia state) during the expeditions

Northeast Score I, II, III and IV (NE I, II, III and IV) (1995–2000); these collections were funded by the Brazilian Government and conducted from the RV ‘Antares’ (Directorate of Hydrography and Navigation). The material was collected using a dredge with a mesh size of 0.5 mm and capacity of about 70 L of sediment. Body length was measured from the anterior margin of the rostrum to the tip of the telson in lateral view to avoid bias from a flexed body posture. Body width was measured on the widest part of the carapace in dorsal view. Terminology follows Larsen (2003). Adjectives such as short and long are quantifies relative to the appendages on they are located. Dissections were made with chemically-sharpened tungsten wire needles and then placed on slides with glycerine, covered by a cover slip and sealed with nail polish. Whole-animal illustrations were made from holotype while appendages were dissected and drawn from paratypes via a camera lucida attached to a Leica compound microscope. Type material is kept at the Carcinological Collection of the ‘Museu de Oceanografia Petrônio Alves Coelho’, Universidade Federal de Pernambuco, Recife, Brazil (MOUFPE).

Results and Discussion

Systematics

Order Tanaidacea Dana, 1849

Suborder Tanaidomorpha Sieg, 1980b

Family Paratanaidae Lang, 1949

Genus *Paratanais* Dana, 1852

Paratanais coelhoi **n. sp.**

(Figures 7–8)

Type material: Holotype: one adult female without oostegites, 1.9 mm [MOUFPE 14.385]. Collected from sand sediment on 20th November 2000, station NE IV #131; 02°13’48’’S 39°53’24’’W. Depth 40 m.

Paratypes: one adult female with oostegites (dissected) [MOUFPE 14.386]. Eight adult females without oostegites [MOUFPE 14.387], same locality. Type locality: Ceará state, continental shelf, Brazil.

Diagnosis: Pleonites 1–4 with lateral circumplumose setae while 5th with simple seta. Antennule article 1 stout, about 1.3 times as long as wide; article 2 at least twice as wide as long. Antenna article 2 about 1.2 times as long as wide. Maxilliped palp article 2 with three inner distal simple setae which distal one is stouter, no spiniform serrated seta present. Cheliped propodus with one outer ‘S’-shaped broad seta and one inner bipinnate seta; fixed finger with five denticles. Pereopod 1 merus 1.7 times as long as wide; pereopod 2 merus without ventral spiniform seta; pereopods 4–6 with three to four distal carpal spiniform setae. Uropod endopod biarticulate, exopod uniarticulate, about 1.2 times as long as first article of endopod.

Etymology: This species is named in honour of the recently deceased Professor Petrônio Alves Coelho, in recognition of his many contributions to crustacean research in Brazil.

Description: Based on holotype (length, 1.9 mm) and paratype. Paratype, adult female with oostegites (body measurements extracted from the holotype and dissected appendages of the paratype).

Body (Figure 7A): dorsoventrally flattened, about 6.9 times as long as wide. Cephalothorax: about 1.2 times as long as wide, naked. Rostrum blunt and rounded at tip. Pereon: straight and naked, about 4.3 times as long as wide and about 62% of total body length. Pereonites 1–6 respectively, 0.5, 0.8, 0.8, 0.8, 0.8 and 0.7 as long as wide. Pleon as wide as pereonites 5–6, about 21% of total body length. Pleonites 1–5 subequal, with circumplumose setae on lateral margins of pleonites 1–4 while simple on 5^{th} pleonite. Pleotelson (Figure 7B) as long as two first pleonites combined, with two pairs of simple setae on posterior margin.

Antennule (Figure 7I): article 1 stout, about 1.3 as long as wide, outer distal margin with four setulated and two simple setae, one simple seta on inner distal margin. Article 2 about 0.4 times as long as wide, with two setulated setae on inner distal margin. Article 3 naked, about 0.6 times as long as wide. Article 4 slender, about 0.9 times as long as article 1 and 3.1 times as long as wide, with one outer distal simple seta. Article 5 minute, with one simple seta and two aesthetascs on distal margin.

Antenna (Figure 7J): article 1 short, with one simple seta on inner distal margin. Article 2 about 1.2 times as long as wide, with one tiny spiniform seta on outer distal margin and one simple seta on inner distal margin. Article 3 about 0.6 times as long as article 2, with one long spiniform seta on outer distal margin. Article 4 longest, about 2.5 times as long as wide, with one pair of setulated setae on each distal margin. Article 5 with two simple setae on outer distal margin. Article 6 minute (hardly visible), with three long simple setae on distal margin.

Mouthparts (Figure 7C–H): labrum (Figure 7H) typical of genus, rounded with several fine simple setae distally. Mandibles (Figure 7C, D) left mandible molar process with notch in the middle and two ‘tooth-like’ projections in middle; right mandible with molar process broad and denticles on distal margin. Left mandible (Figure 7C) incisor as long as lacinia mobilis with six distal denticles, lacinia mobilis flattened with eight distal denticles. Right mandible (Figure 7D) incisor broad, with seven denticles on distal margin. Labium (Figure 7E) with fine simple setae on anterior and lateral margins. Maxillule (Figure 7G) slender, palp uniarticulate (not illustrated). Endite with fine setae on outer and ventral margins, with seven spiniform setae on distal margin. Maxilliped (Figure 7F) endite broad, with short spines (hardly visible) and one fine simple seta on outer distal margin, inner distal margin with two flattened setae and one long simple seta. Basis with one distal simple seta. Palp article 1 naked, about 1.2 times as long as wide; article 2 slightly longer than article 1, with one simple seta on outer distal margin and three inner distal simple setae which distal one stouter (spiniform serrated seta absent); article 3 with three bipinnate setae on inner distal margin; article 4 short, inner distal margin with five bipinnate setae and four fine setae, one outer distal simple seta. Epignath not recovered.

Cheliped (Figure 7K): attached via triangular sclerite (not illustrated). Basis short, with one dorsodistal simple seta, about 1.2 times as long as wide. Merus triangular, with one ventromedial simple seta. Carpus about 1.8 times as long as wide, dorsal margin with one proximal and one distal simple seta, one pair of ventromedial simple setae. Propodus with one ‘S’-shaped broad outer distal seta, inner margin with one bipinnate seta and a row of fine setae. Dactylus with one dorsal simple seta, unguis slightly curved internally. Fixed finger with two ventral simple setae, inner margin with five denticles and three simple setae. Unguis well developed.

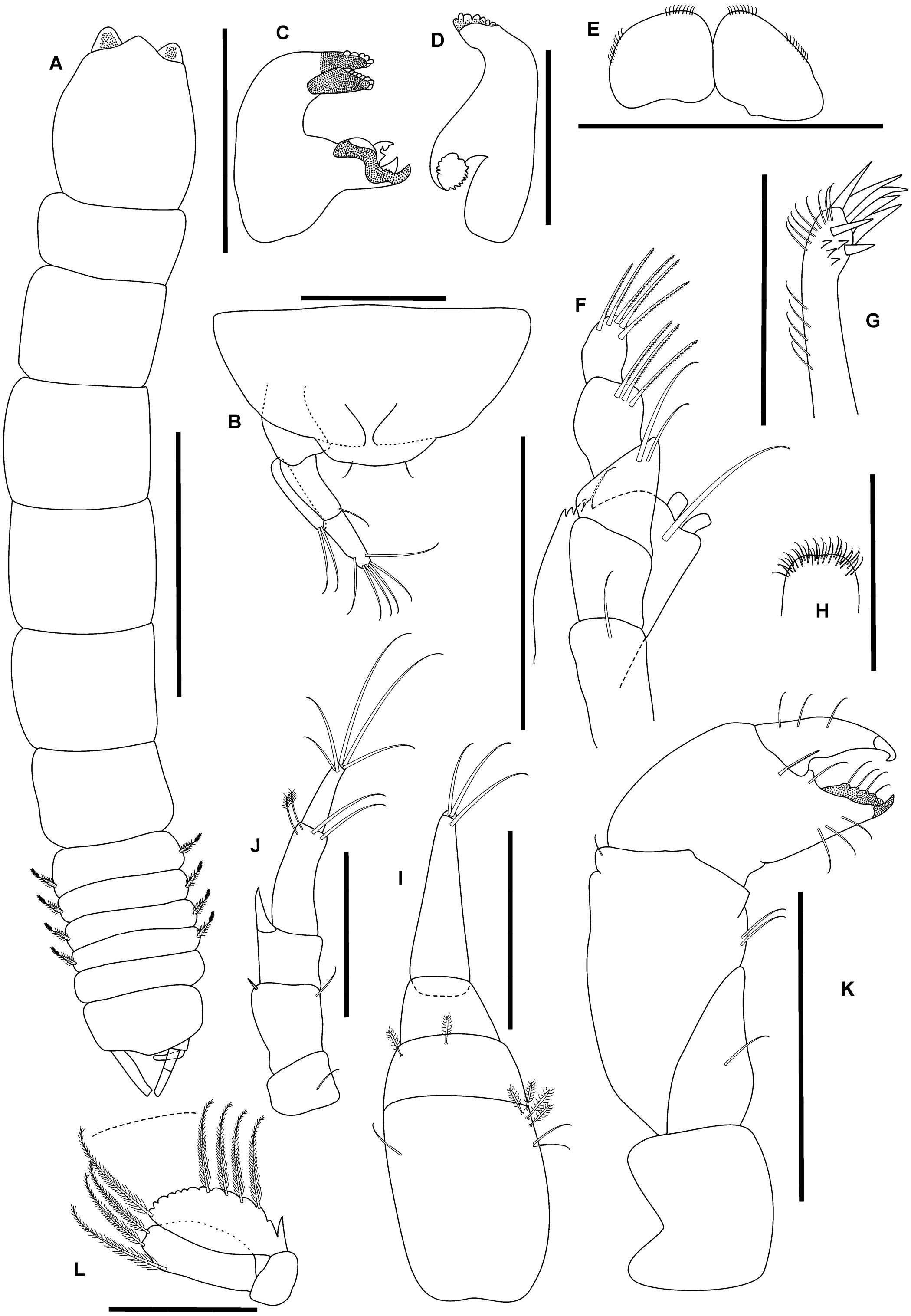


Figure 7. *Paratanais coelhoi* n. sp., adult female, holotype and paratype [MOUFPE 14.385 and 14.386, respectively]. Holotype: (A) Dorsal view. Paratype: (B) pleotelson and uropod; (C) left mandible; (D) right mandible; (E) labium; (F) maxilliped; (G) maxillule; (H) labrum; (I) antennule; (J) antenna; (K) cheliped; (L) pleopod. Scale bars: (A) = 0.5 mm; (B–J, L) = 0.1 mm; (K) = 0.2 mm.

Pereopod 1 (Figure 8A): coxa with one simple seta. Basis slender, about 3.4 times as long as wide, with one dorsoproximal simple seta. Ischium with one ventral simple seta. Merus about 1.7 times as long as wide, as long as carpus, with one ventrodistal simple seta. Carpus with two dorsodistal simple setae and one ventrodistal simple seta. Propodus about 3.1 times as long as wide, with two dorsodistal simple setae and one ventrodistal simple seta. Dactylus and unguis combined as long as propodus. Unguis about twice as long as dactylus.

Pereopod 2 (Figure 8B): coxa as pereopod 1. Basis about 2.7 times as long as wide, with one dorsoproximal simple seta. Ischium as pereopod 1. Merus short, about 1.2 times as long as wide, with two ventrodistal simple setae (spiniform seta absent). Carpus as long as merus, each distal margin with one spiniform and one simple seta. Propodus about 2.5 times as long as wide, with one simple seta on dorso and ventrodistal margins. Dactylus and unguis as pereopod 1.

Pereopod 3 (Figure 8C): as pereopod 2 except merus ventrodistal margin with one spiniform and one simple seta. Carpus without simple setae, with scale and one pair of ventrodistal spiniform setae.

Pereopod 4 (Figure 8D): no visible coxa. Basis naked, robust, about 1.8 times as long as wide. Ischium with two ventral simple setae. Merus ventrodistal margin with a row of fine setae and two spiniform setae. Carpus as long as merus, with one dorsodistal simple seta and two spiniform setae on each distal margin, at least two of which have medial ring of spinules. Propodus about 2.6 times as long as wide and 1.8 times as long as dactylus and unguis combined, with one dorsomedial setulated seta and one dorsodistal spiniform seta as long as dactylus and unguis combined, one shorter ventrodistal spiniform seta. Dactylus and unguis combined shorter than previous pereopods. Unguis short and incompletely fused with dactylus.

Pereopod 5 (Figure 8E): as pereopod 4 except carpus with one ventrodistal spiniform seta with medial ring of spinules. Propodus dorsal margin with one medial setulated and one distal spiniform seta, ventrodistal margin with two pinnate spiniform setae and one tiny spiniform seta.

Pereopod 6 (Figure 8F): as pereopod 5 except propodus without dorsomedial setulated seta, with three dorsodistal pinnate spiniform setae, one ventrodistal spiniform seta and one simple seta next to insertion of dactylus.

Pleopods (Figure 8L): basal article naked. Endopod as long as exopod, with 11 outer plumose setae, one inner plumose seta and fine setae on outer margin. Exopod with 14 outer plumose setae.

Uropod (Figure 8B): basal article naked. Endopod biarticulate; article 1 with one simple seta; article 2 with six distal simple setae. Exopod uniarticulate, about 1.2 times as long as article 1 of endopod, with two distal simple setae.

Remarks: Silva-Brum (1973: 4) observed differences on the molar process and endite of maxilliped between *P. oculatus* (*sensu* Silva-Brum, 1973) and *P. oculatus* (*sensu* Vanhöffen, 1914). However, the author considered these features insufficient to erect a new species or synonymize *P. euelpis* Barnard, 1920 as suggested by Lang (1950: 360). It is somehow a bit confusing why the author considered the specimens from Brazil as *P. oculatus sensu stricto* (Vanhöffen, 1914) and not *P. euelpis* if we take into account their geographic distribution.

To separate *P. oculatus* (*sensu* Vanhöffen, 1914) and *P. euelpis*, Sieg (1986: 57) remarked that both species are distinct by the length merus of pereopod 1 and the shape of the distolateral margin of the maxillipedal endite; the author also considered *P. oculatus* (*sensu* Silva-Brum, 1973) a misidentification, based on the distribution of *P. oculatus*, since the species was only recorded from the Subantarctic (Kerguelen and Falkland Islands) and Indian Ocean while *P. euelpis* from Cape Town (South Africa) and Morocco (Monod 1925: 65). Currently, Bird (2011) regards the records of *P. oculatus* in New Zealand waters by Sieg (unpublished data) as unconfirmed.

Considering their distribution it seems unlikely that they are the same species, however, until a close examination of the material we will here consider the species remarked by Silva-Brum (1973) as *P. oculatus*.

Recently Bird (2011) regarded that most of the species assigned to the genus *Paratanais* do not conform to the pattern set by the type species *P. elongatus* (Dana, 1849) with respect to pereonite proportions, pleonal plumose setation (1–4), cheliped shape and pereopod setation. Our observations confirm this differences (see Table 1).

With concern to the lateral circumplumose epimeral setae on pleonites 1–4 while simple seta on 5th and the maxillipedal palp setation, *P. coelhoi* n. sp. is similar to *P. gaspodei* Bamber, 2005, *P. wanga* Bamber, 2008, *P. martinsi* Bamber

& Costa, 2009 and *P. vicentetis* Larsen, 2012. However it can be distinguished by these and other closely related species as *P. euelpis*, *P. oculatus* (Vanhöffen, 1914 *sensu* Silva-Brum, 1973), *P. oculatus* (*sensu* Shiino, 1978) and *P. tara* Bird, 2011 by the unique following combination of characters: 1) the pleonites 1–4 with lateral circumplumose setae while one simple on 5^{th} [pleonites 1–4 circumplumose in *P. tara*, simple (appears simple in Shiino, 1978: 68, fig. 38B) and naked in *P. oculatus* (*sensu* Silva-Brum, 1973)]; 2) the antennule article 1 stout, about 1.3 times as long as wide [while 2.3, 2.5, 1.5 and 1.9 times in *P. euelpis*, *P. oculatus* (*sensu* Shiino, 1978), *P. oculatus* (*sensu* Silva-Brum, 1973) and *P. tara*, respectively]; 3) the maxilliped palp article 2 with three inner distal simple setae which distal one is stouter but without serrated spiniform seta; 4) the cheliped propodus with one outer 'S'-shaped broad seta and one inner bipinnate seta; 5) the cheliped fixed finger with five denticles (in most *Paratanais* species the incisive margin is coarser with massive distal denticle/tooth); 6) the pereopod 1 merus 1.7 times as long as wide (at least two times as long as wide in related species); 7) the pereopod 2 merus without ventral spiniform seta (unusual in most *Paratanais* species which usually have one spiniform seta); 8) the uropod endopod biarticulate, exopod uniarticulate, about 1.2 times as long as first article of endopod (for an extensive comparison with other species, see Table 1).

Paratanais spinanotandus Sieg, 1981 is recorded for South Africa (Seamount Vema), but is easily distinguished from *P. coelhoi* by the serrate spiniform seta [referred as 'spine' by Sieg (1981)] on the article 2 of the maxillipedal palp, by the proportion of the P1 merus (3.9 times as long as wide), and by the uropodal exopod length relative to that of endopod article 1.

It is possible that *P. oculatus* (*sensu* Silva-Brum, 1973) is conspecific with *P. coelhoi*, but the specimens are kept on 'Museu Nacional do Rio de Janeiro' (MNRJ) and could not be obtained for this study.

There are a few anomalies regarding *P. impressus* Kussakin & Tzareva, 1972. The authors figured the pereon with seven pereonites which is clearly a fusion of the cephalon with first pereonite.

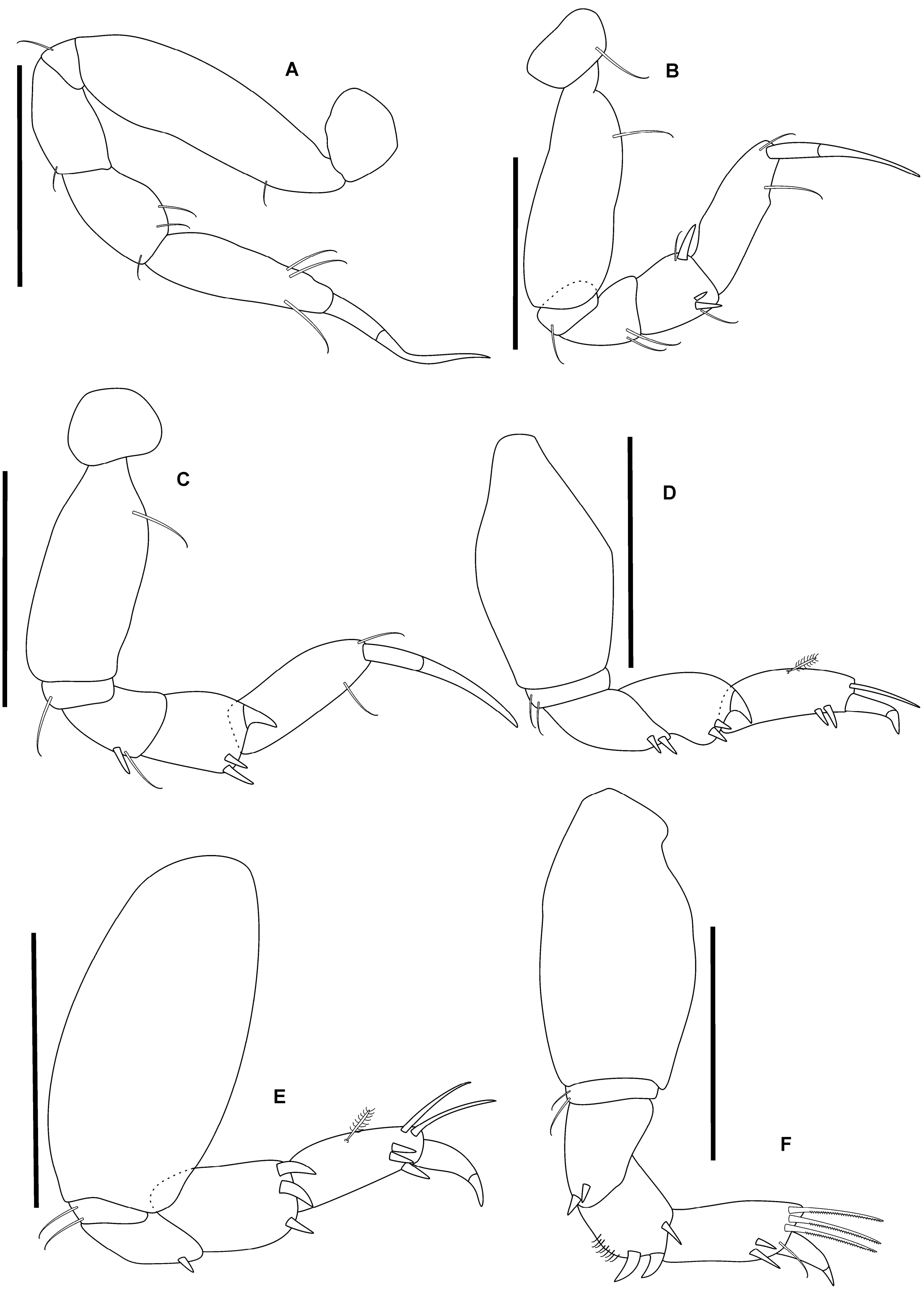


Figure 8. *Paratanais coelhoi* n. sp., adult female, paratype [MOUFPE 14.386]. (A) Pereopod 1; (B) pereopod 2; (C) pereopod 3; (D) pereopod 4; (E) pereopod 5; (F) pereopod 6. Scale bars: (A–F) = 0.1 mm.

Table 1. List of mainly diagnostic characters of all described *Paratanais* Dana, 1852 species, modified from Bird (2011). Abreviations: prop.=proportion; chel.=cheliped; per.=pereopod; maxillip.=maxilliped; pereon.=pereonite; A1=antennule; art.=article; exop.=exopod; end.=endopod; circum.=circumplumose; Chel.= cheliped; Max. = Maxilliped; set. = setation

Taxa	Type locality	Size of adult female	Pereonites 1–6 prop.	Prop. pereon. 5–6 to pleon	Pleonal setation	Prop.of A1 1st art.	Prop. of A2 art. 2	Max. palp set.	Maxillip. endite set.	Chel. prop. of basis & carpus	Chel. propod set.	Prop. of P1 merus	Carpal spines of per. 4–6	Uropod endopod	Uropod exopod	Uropod exop/end.
Paratanais clarkae Bird&Bamber, 2000	IndoPacific (South China Sea)	3.8 mm	5.2x (0.69; 0.9; 0.9; 0.9; 0.7)	As wide as	1–5(all circum.)	1.7x	1.6x	Simple and bipinnate	1 short simple seta	basis: 1.8x; carpus: 1.3x	2 comb setae	2.8x	2–3	Biarticulate	Uniarticulate	0.9x
P.coelhoi **sp.nov**	Ceará, Brazil	1.9 mm	4.3x (0.5; 0.82; 0.86; 0.83; 0.83; 0.74)	As wide as	1–4(1 simple seta on 5th pleonite)	1.3x	1.2x	Simple and bipinnate	1 long simple seta	1.2x; 1.8x	1 stout simple seta and 1 bipinnate	1.7x	3–4	Biarticulate	Uniarticulate	1.2x
P.denticulatus Guţu&Ramos, 1995	Eeast Pacific (Colombia)	4.2 mm	2.7x (0.35; 0.34; 0.45; 0.51; 0.51; 0.6)	0.9 times as wide as pleon	1–4 (simple seta?)	1.7x	1.7x	Bipinnate and stout serrated spiniform	1 long simple seta	1.1x; 1.3x	Naked	2.5x	4	Biarticulate	Uniarticulate	1.3x
P.elongatus (Dana, 1849 *sensu* Bamber, 1998)	Indo-Pacific Sulu Archipelago)	2.3 mm	5.4x (0.4; 1.1; 1.1; 1.0; 1.0; 0.8)	As wide as	1–4 (circumpl. (Bird, 2011)	2x	2x	Simple and bipinnate	1 long simple seta	1.9x; 1.6x	2 bipinnate setae and 1 simple seta	2.1x	3–4	Biarticulate	Uniarticulate	0.6x ?
P.euelpis Barnard, 1920 *sensu* Lang, 1973	Cape Town (South Africa)	4–6 mm (*Barnard, 1920)	2nd slightly shorter than 3rd; 3rd and 4th subeq.; 5th and 6th subeq. (*Barnard, 1920)	As wide as	unknown	2.3x	1.6x	Apparent 3 simple setae	1 long simple seta	1.2 1.4x	2 pi-binnate setae?	3x	4	Biarticulate	Uniarticulate	0.8x
P.gaspodei Bamber, 2005	Western Australia	2.8 mm	4x (0.5; 0.6, 0.72; 0.8; 0.85; 0.8)	0.9 times As wide as pleon	1–4 (1 simple seta on 5th pleonite)	1.7x	1.2x (with lateral projections)	Simple and pinnate	1 short simple seta	1.3x; 1.3x	1 short simple seta	2.8x	2	Biarticulate	Uniarticulate	0.8x
P.hessleri Kudinova-Pasternak, 1985	N. Atlantic (Great Meteor Seamount)	3.6 mm (?)	4.4x (0.55; 0.74; 0.85; 0.88; 0.87; 0.7)	As wide as	1–5 (simple seta?)	2.1x	1.5x	Simple and bipinnate	1 short simple seta	1.2x; 1.85x	Naked	3x	4	Biarticulate	Biarticulate	0.9x
P.impressus Kussakin&Tzareva, 1972	N.Pacific (Kurile Islands)	5.5 mm	2.7x (0.3; 0.4; 0.36; 0.4; 0.5; 0.38; 0.34)	As wide as	Naked	2x	1.5x	Simple and bipinnate	1 short simple seta	1.3x; 1.4x	1 simple seta	Unknown	3	Biarticulate	Uniarticulate	As long as
P. intermedius Dojiri & Sieg, 1997	Eeast Pacific (California)	2.1 mm	3.4x (0.43; 0.56; 0.77; 0.88; 0.76; 0.42)	As wide as	Naked	2.1x	1.5x	Simple, bipinnate and serrated	1 short simple seta	1.3x; 1.4x	Naked	1.8x	2–3	Biarticulate	Uniarticulate	As long as
P.maleficus Larsen, 2001	Botany Bay, Australia	3.7 mm	4.1x (0.5; 0.68; 0.7; 0.83; 0.9; 0.75)	As wide as	1–5 (all circumpl.)	2x	1.1x	Serrated and bipinnate	1 short simple seta	1.4x; 1.7x	Naked	2.3x	3	Biarticulate	Biarticulate	As long as
P.malignus Larsen, 2001	Botany Bay, Australia	3.1 mm	3x (0.3; 0.48; 0.57; 0.6; 0.65; 0.55)	As wide as	1–5 (all circumpl.)	1.8x	2x	Serrated and bipinnate	Naked	1.7x; 1.8x	1 short serrate seta	3x	2	Biarticulate	Uniarticulate	As long as
P.martinsi Bamber & Costa, 2009	N. Atlantic, Azores, Portugal	4.2 mm	5.1x (0.62; 0.85; 1.0; 1.16; 1.08; 0.81)	As wide as	1–4 (1 simple seta on 5th pleonite)	2.2x	1.2x (with lateral projections)	Simple and bipinnate	1 short simple seta	1.4x; 1.7x	3 short simple? setae	4.1x	3–4	Biarticulate	Uniarticulate	0.7x
P.monodi	Red Sea	Unknown	Unknown	Unknown	Unknown	2.1x	0.8x	Unknown	Unknown	Unknown	Unknown	Unknown	Unknown	Biarticulate	Uniarticulate	0.9x

Makkaveeva, 1971																
P.oculatus (Vanhöffen, 1914 *sensu* Shiino, 1978)	Kerguelen Islands	6.4 mm	3.4x (0.54; 0.64; 0.61; 0.7; 0.68; 0.54)	Slightly wider than pereon	1–5 (simple seta?)	2.5x	2.2x	Simple and bipinnate	Naked?	1.2x; 1.8x	2 simple setae	3.4x	2–3	Biarticulate	Biarticulate	As long as
P.oculatus (Vanhöffen, 1914 *sensu* Silva-Brum, 1973)	Ilha Redonda, Bahia, Brazil	3.7 mm	3.8x (0.41; 0.54; 0.65; 0.73; 0.76; 0.59)	As wide as	Naked	1.5x	0.9x	Unknown	Unknown	1.3x; 1.4x	Naked	2x	Unknown	Uniarticulate	Uniarticulate	0.6x
P. paraoa Bird, 2011	Armer's Bay, NZ	2.6-3.34 mm	3.8x (0.41; 0.55; 0.57; 0.59; 0.77; 0.57	0.9 times as wide as pleon	1–4 (circumpl.)	2x	1x (with lateral projections)	Simple and bipinnate	1 short simple seta	1.2x; 1.7x	1 simple seta	2.4x	4	Biarticulate	Biarticulate	As long as
P.perturbatius Larsen, 2001	Botany Bay, Australia	2.6 mm	4.4x (0.5; 0.72; 0.81; 0.9; 0.81; 0.71)	As wide as	Naked	1.1x	1.4x	Serrated and bipinnate	1 short simple seta	1.4x; 1.6x	Naked	2.5x	3	Biarticulate	Uniarticulate	0.8x
P. spinanotandus Sieg, 1981	Seamount Vema, S.Africa	3 mm	2.6x(0.3; 0.37; 0.45; 0.45; 0.48; 0.38)	As wide as	Naked	2x	1.5x	Simple, bipinnate and spiniform serrated	1 short simple seta	1.7x; 1.6x	2 simple seta	3.9x	3 to 4	Biarticulate	Uniarticulate	0.8x
P. tara Bird, 2011	NZ	1.4-3.6 mm	4.2x(0.43; 0.78; 0.77; 0.79; 0.82; 0.68)	As wide as	1–4 (circumpl.)	1.9x	1x (with lateral projections)	Simple and bipinnate	1 short simple seta	1.4x; 1.7x	2 simple setae and 3 bipinnate	1.9x	4	Biarticulate	Uniarticulate	1.2x
P. vetinari Bamber, 2005	Western Australia	4.8 mm	2.9x (0.34; 0.5; 0.55; 0.6; 0.58; 0.5)	As wide as	1–5 (all circumpl.)	1.6x	1.3x	Simple and pinnate	1 short simple seta	1.3x; 1.7x	Naked	2.7x	3	Biarticulate	Biarticulate	1.3x
P.vicentetis Larsen, 2012	Cape Verde Archipelago	3.5 mm	3x (0.5; 0.6; 0.5; 0.57; 0.6; 0.36	As wide as	1–4 (1 simple seta on 5th pleonite)	1.4x	1x (with lateral projections)	Bipinnate and serrated spiniform	1 short simple seta	1.3x; 1.7x	1 stout simple seta	1.9x	3–4	2 pseudoarticles	Uniarticulate	As long as
P. wanga Bamber, 2008	Moreton Bay, Australia	3.4 mm	3.2x(0.37; 0.52; 0.5; 0.61; 0.59; 0.57)	As wide as	1–4 (1 simple seta on 5th pleonite)	1.6x	1.6x	Simple and pinnate	1 short simple seta	1.4x; 1.7x	3 short simple? setae	2.6x	2	Uniarticulate	Uniarticulate	0.5x

New Records

Family Apseudidae Leach, 1814

Genus *Paradoxapseudes* Guţu, 1991

Paradoxapseudes intermedius (Hansen, 1895)

Apseudes intermedius Hansen, 1895: 49, 50; Băcescu, 1961: 152–156; Silva-Brum, 1969: 601, 602; Gardiner, 1975: 205.

Muramura intermedia: Guţu, 2006: 84.

Gollumudes intermedius: Guţu, 2007: 55, 56.

Paradoxapseudes intermedius: Guţu, 2008: 23, 24, 28, 29; Anderson, 2012: 3.

Muramurina intermedia: Larsen *et al*., 2009: 2.

Type locality: Cape Verde Islands.

Material examined: One adult female, ovigerous (damaged) [MOUFPE 14.291]. Collected on 11 December 2000, station NE IV #109A; 1°45'S 37°6'W, off Ceará state, North Chain Banks, Brazil. One adult female without oostegites (damaged) [MOUFPE 14.292]. Collected on 4th December 2000, station NE IV #181; 11°54'S 37°24'W, Bahia state, continental shelf.

Geographic distribution: Northwestern Atlantic: Mediterranean Sea (Larwood 1940), Morocco (Monod 1925) and Cape Verde Islands (Hansen 1895). Southwestern Atlantic: continental shelf of Ceará and Bahia states (present study), Rio de Janeiro (Silva-Brum 1969), Brazil.

Remarks: The specimens were dredged between 40.5 and 51 m depth, and were sorted from algae and sponges. The individuals correspond to the original description, except for the cephalothorax width being slightly wider than first pereonite and antennule with 16 articles in the outer flagellum (seven in *Paradoxapseudes intermedius sensu* Guţu, 2008). This is the first record of *P. intermedius* from northeastern Brazil.

Family Leptocheliidae Lang, 1973

Genus *Intermedichelia* Guţu, 1996

Intermedichelia gracilis Guţu, 1996

Intermedichelia gracilis Guţu, 1996: 111–120; Larsen & Wilson, 2002: 208, 211, 214; Larsen *et al*., 2009: 2; Anderson, 2012: 19.

Type locality: Cabo Frio, Rio de Janeiro, Brazil.

Material examined: One adult female (ovigerous) [MOUFPE 14.321]. Collected on 14 November 2000, station NE IV #130;03°20'24''S 38°10'48''W, Ceará State, continental shelf. One adult female without oostegites [MOUFPE 14.322]. Collected on 3rd December 2000, station NE IV #178; 11°16'12''S 37°01'12''W, Sergipe state, continental shelf.

Geographic distribution: Southwestern Atlantic: continental shelf of Ceará and Sergipe states (present study), Cabo Frio, Rio de Janeiro, Brazil (Guţu, 1996).

Remarks: The specimens examined in this study were dredged between 70.8 to 71.6 m depth, from sandy sediments, and were sorted from algae and sponges. *Intermedichelia gracilis* is endemic to Brazilian waters and this is the first record of the species from northeastern Brazil.

Family Leptognathiidae Sieg, 1976

Genus *Biarticulata* Larsen & Shimomura, 2007

Biarticulata sp.

(Figure 9A, B)

Material examined: One adult female without oostegites, 2.2 mm [MOUFPE 14.377]. Collected on 12 November 2000, station NE IV #113A; 01°37'12''S 38°07'12''W, off Ceará state, North Chain Banks, Brazil. One adult female (damaged) [MOUFPE 14.378] same locality.

Geographic distribution: Southwestern Atlantic: off Ceará state, North Chain Banks, Brazil.

Remarks: The specimens were found on gravel bottom, at 47.7 m depth, temperature of 26°C and salinity of 36. The genus *Biarticulata* Larsen &

Shimomura, 2007 is characterized by the biarticulation on the uropod exopod; however, the authors emphasized that this character is probably homoplastic and considered the genus clearly paraphyletic, thus *Biarticulata* was erected to separate species with this character (Larsen & Shimomura 2007: 19) from other leptognathids.

Biarticulata sp. has the uropod exopod biarticulate, however differs from *Biarticulata elegans* Kudinova-Pasternak, 1965, *B. greveae* Kudinova-Pasternak, 1976, *B. parabranchiata* Kudinova-Pasternak, 1977, *B. mironovi* Kudinova-Pasternak, 1981, mainly with respect on the uropod exopod length with 0.4 times as long as first endopod (versus 0.56, 0.6, 0.3, 0.7 times as long as first endopod in *B. elegans*, *B. greveae*, *B. parabranchiata* and *B. mironovi*, respectively); the uropod endopod uniarticulate in *Biarticulata* sp. (Figure 9B) (versus biarticulate in all *Biarticulata* species related). This is the first record of the family Leptognathiidae in Brazilian waters.

Family Metapseudidae Lang, 1970

Genus *Vestigiramus* Guţu, 2009

Vestigiramus sp.

(Figure 10A–C)

Material examined: One adult male, 2.1 mm [MOUFPE 14.307]. Collected on 3rd December 2000, station NE IV #178; 11°16’12’’S 37°01’12’’W, Sergipe state, continental shelf.
Geographic distribution: Southwestern Atlantic: Sergipe state, continental shelf, Brazil.

Remarks: The specimen was collected at 71.6 m depth on sandy bottom associated with sponge and algae. Guţu (2009) erected the genus to include *Vestigiramus antillensis* Guţu, 2009 and *V. codreanui* (Guţu, 1996) which have reduced cheliped exopod. The single specimen examined in this study share this and other diagnostic character (Figure 10C), and it is closely related with *V. codreanui* (type locality Santa Catarina, Brazil), however they can be distinguished mainly by *Vestigiramus* sp. having four plumose setae on medial lateral margin of cephalothorax (Figure 10A, B), mandible article 1 with one inner distal spiniform seta, cheliped carpus with eight plumose setae on dorsal margin as well as other characters. This is the first record of the genus for northeastern Brazil.

Family Nototanaidae Sieg, 1976

Genus *Nototanoides* Sieg & Heard, 1985

Nototanoides cf. *trifurcatus* Sieg & Heard, 1985

(Figure 11A, B)

Nototanoides trifurcatus Sieg & Heard, 1985: 51–62; Heard *et al*., 2003: 123, 124, 126; Larsen, 2005: 268; Anderson, 2012: 23.

Type locality: The coast off Texas, East Flower Garden Bank, 72–190 m, Gollums Lake.

Material examined: Two adult males (damaged) MOUFPE 14.380]. Collected on 7th June 1998, station NE III #77A; 01°37'48''S 38°10'12''W, off Ceará state, North Chain Banks, Brazil.

Geographic distribution: Northwestern Atlantic: the coast off Texas. The species is widespread in the northern Gulf of Mexico but with apparently patchy distribution (Larsen 2005: 268). Southwestern Atlantic: off Ceará state, North Chain Banks, Brazil (present study).

Remarks: The specimens were dredged in 56.7 m depth, gravel bottom, temperature 28°C and salinity 36. The two individuals examined are damaged, but when compared with the characters described by Sieg & Heard (1985) and Larsen (2005) shows that the specimens are at least closely related. The differences from the original species are the anterior spiniform projection on eyes lobes and the conformation of the pleotelson (Figure 11A, B), which is more expanded than in *Nototanoides trifurcatus* sensu Sieg and Heard, 1985. This is the first record of *N. trifurcatus* from Brazil, indeed the first record for the entire South Atlantic.

Family Tanaellidae Larsen & Wilson, 2002

Genus *Arhaphuroides* Sieg, 1986

Arhaphuroides sp.

(Figure 9C, D)

Material examined: One adult female without oostegites, 1.57 mm [MOUFPE 14.390]. Collected on 10th April 1997, station NE II #190; 09°49'S 35°39'W, Alagoas state, continental shelf, Brazil.

Geographic distribution: Southwestern Atlantic: continental shelf of Alagoas state, Brazil.

Remarks: The individual was collected at 35 m depth (Figure 9C). This specimen is closely related to *Arhaphuroides io* (Bamber, 2005) and *A. septentrionalis* Sieg & Dojiri (1989) with type locality in Esperance Bay (Western Australia) and coast of New Jersey (NW Atlantic), respectively. Despite the overall similarity, *A. io* has a longer and 'sharper' exopod and a shorter endopod (*Arhaphuroides* sp. uropod endopod 3.2 times as long as wide); no tubercles on cheliped propodus while is evident in *Arhaphuroides* sp. as well as other characters.

Arhaphuroides septentrionalis is distinct from *Arhaphuroides* sp. by the following characters: 1) pleonites about three times as long as wide in *Arhaphuroides* sp. (about 4.6 times in *A. septentrionalis*); 2) antennule article 1 about twice as long as wide in *Arhaphuroides* sp. (about 2.5 times in *A. septentrionalis*); 3) cheliped propodus, fixed finger and dactylus with several tubercles (Figure 9D) (absent in *A. septentrionalis*); 4) uropod endopod uniarticulate, about 6.7 times as long as exopod in *Arhaphuroides* sp. (about 2.2 times in *A. septentrionalis*). This is the first record of the genus *Arhaphuroides* from Brazilian waters.

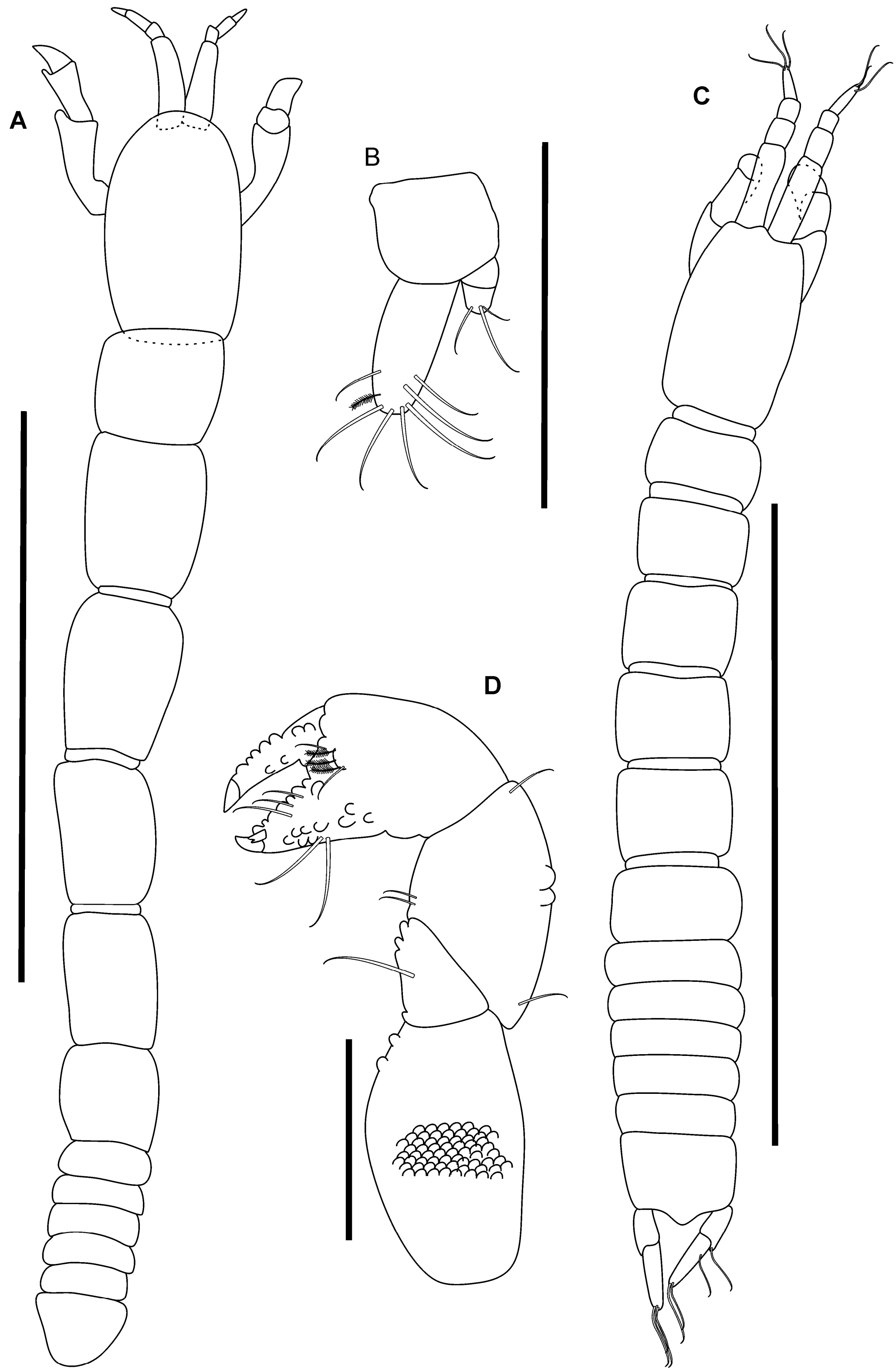


Figure 9. *Biarticulata* sp., adult female with no oostegites [MOUFPE 14.377]. (A) dorsal view; (B) uropod. *Arhaphuroides* sp., adult female with no oostegites [MOUFPE 14.390]. (C) dorsal view; (D) cheliped. Scale bars: (A, C) = 1 mm; (B, D) = 0.1 mm.

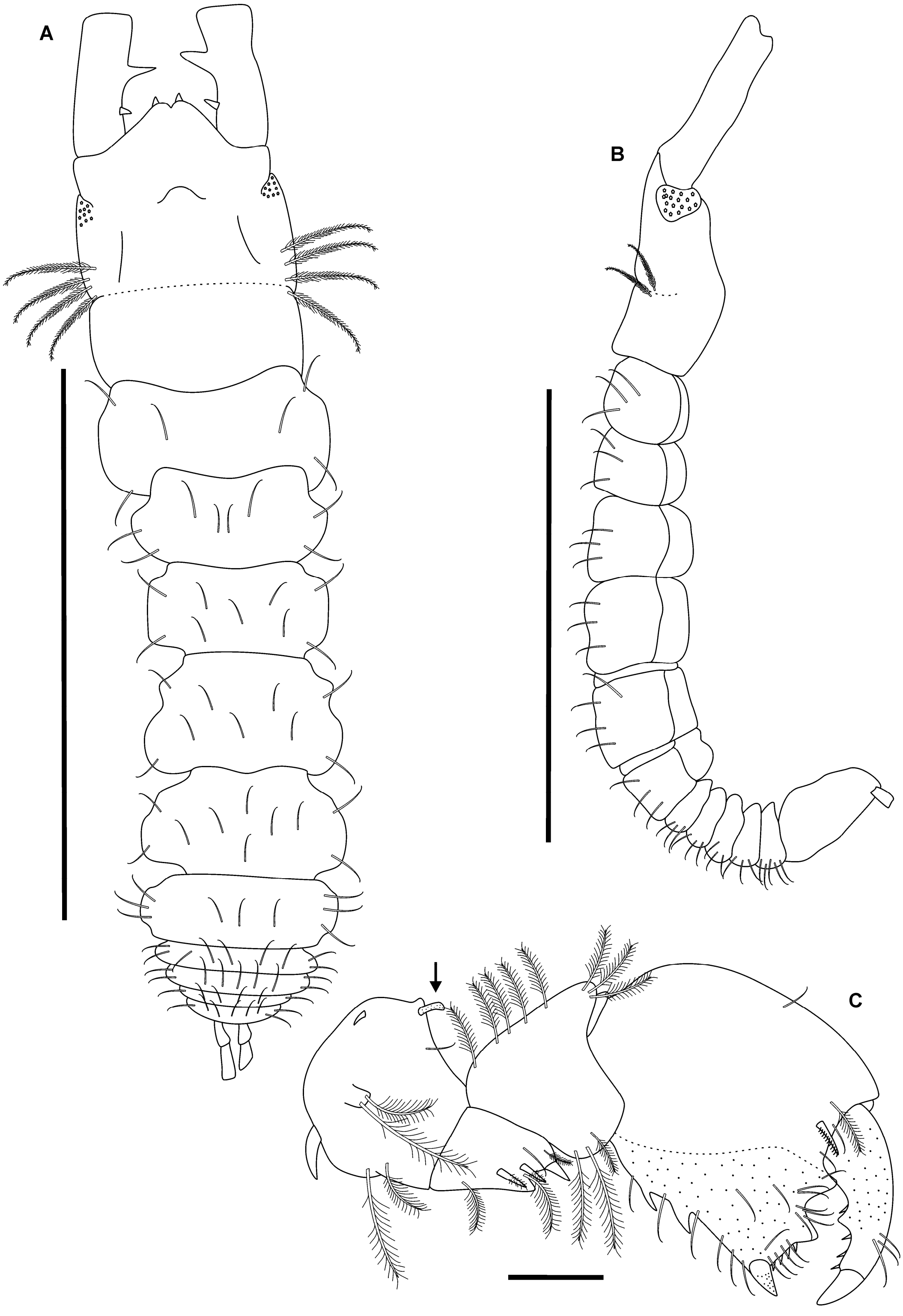


Figure 10. *Vestigiramus* sp., adult male [MOUFPE 14.307]. (A) Dorsal view; (B) lateral view; (C) cheliped; seta indicates the vestigious exopod. Scale bars: (A, B) = 1 mm; (C) = 0.5 mm.

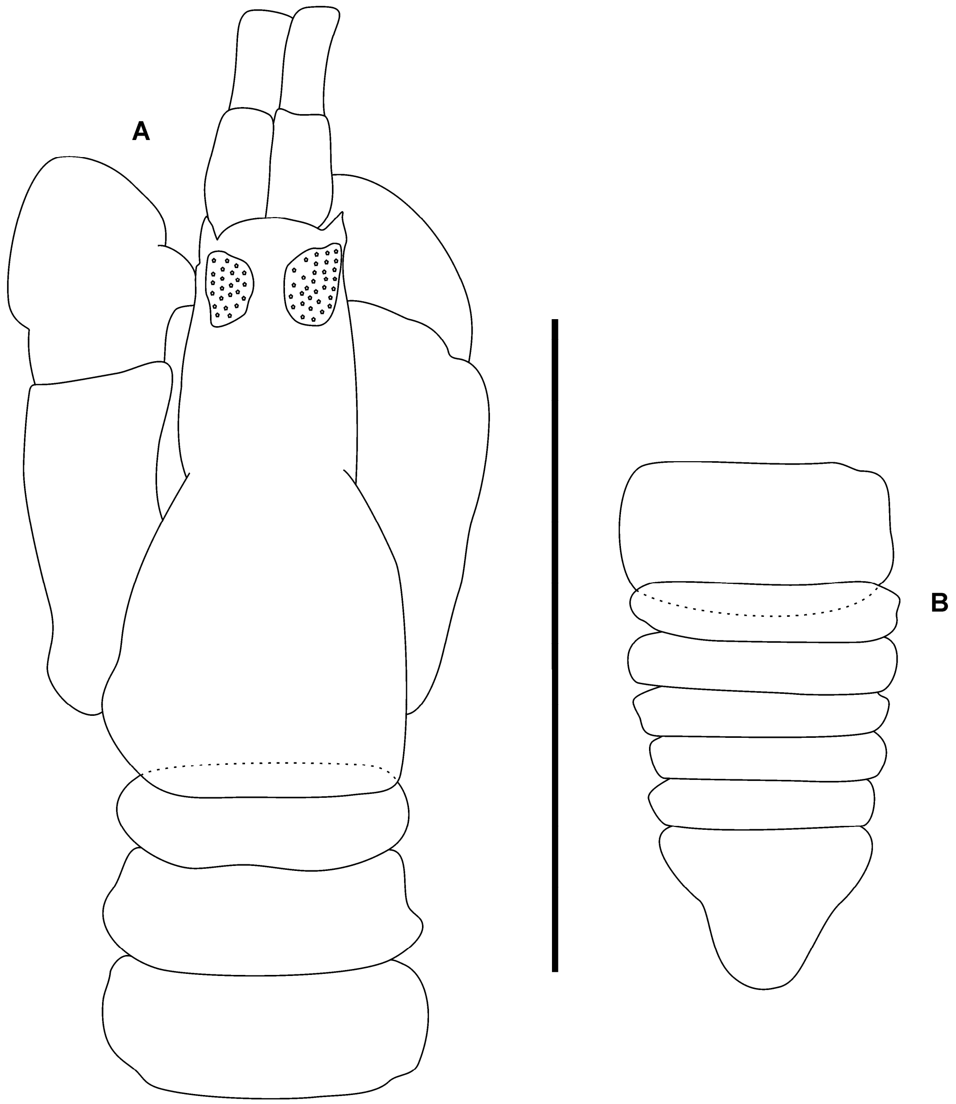


Figure 11. *Nototanoides* cf. *trifurcatus*, adult male [MOUFPE 14.380]. (A) detail of cephalothorax and pereonites; (B) pleon and pleotelson. Scale bar: (A, B) = 1 mm.

Acknowledgments

The authors would like to thank ‘The Brazilian Carcinological Society’ for the invitation and for the initiative in dedicate this special edition to Professor Petrônio Alves Coelho (Universidade Federal de Pernambuco) in recognition of his many contributions to crustacean research in Brazil; also thanks to the criticism of two anonymous reviewers. This paper is part of a Ph.D. dissertation (CLAS) funded by CAPES-Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Scholarship Grant number: 5428/10-6).

References

Anderson, G. (2012). Tanaidacea Classification, February, 2, 2012. Available at: http://peracarida.usm.edu/TanaidaceaTaxa.pdf. p. 1–30. (Accessed on April 2012).

Araújo-Silva, C.L. & Larsen, K. (2010). Tanaidacea from Brazil. II. A revision of the subfamily Hemikalliapseudinae (Kalliapseudidae; Tanaidacea; Crustacea) using phylogenetic methods. *Zootaxa*, 2555: 30–48.

Araújo-Silva, C.L. & Larsen, K. (2012). Tanaidacea (Tanaidacea: Crustacea) from Brazil. IV. A new genus and two new species from the family Leptocheliidae. *Zootaxa*, 3523: 1–19

Băcescu, M. (1961). Contribution a la connaissance des tanaidacés de la Méditerranée orientale- 1: Les Apseudidae et Kalliapseudidae des côtes d´Israel. *The Bulletin of the Research Council of Israel* (Zoology), 10: 137–170.

Băcescu, M. (1979). Kalliapseudes gianucai, a new Tanaidacea from the Brazilian waters. *Revue Roumaine de Biologie (Série de Biologie Animale),* 24 (1): 3–8.

Băcescu, M. (1984). Deux espèces nouvelles d´Apseudoidea (Tanaidacea) de La zone abyssale du NE du Cône de l´Amazone: *Leviapseudes demerarae* sp. n. et *L. preamazonica* sp. n. *Travaux du Muséum National d´Histoire Naturelle 'Grigore Antipa'*, 25: 79–89.

Băcescu, M. (1986). *Heteromysis mureseanui* n. sp. and *Kalliapseudes viridis*, ssp. *brasiliensis* n. ssp., from the Brazilian littoral waters. *Revue Roumaine de Biologie (Série de Biologie Animale),* 31: 93–97.

Băcescu, M. & Absalão, R.S. (1985). *Hemikalliapseudes cavooreni* n. sp. and a few remarks on the Brazilian Apseudoidea. *Travaux du Muséum National d´Histoire Naturelle'Grigore Antipa'*, 27: 49–54.

Bamber, R.N. (1998). Tanaidaceans (Crustacea, Peracarida) from the Southeast of the South China Sea. *Asian Marine Biology*, 15: 169–197.

Bamber, R.N. (2005). *The tanaidaceans (Arthropoda: Crustacea: Peracarida: Tanaidacea) of Esperance, Western Australia, Australia*, Pp. 613–728. *In*: Wells, F.E.; Walker, D.I. & Kendrick, G.A. (eds), The Marine Flora and

Fauna of Esperance, Western Australia. Perth, Western Australian Museum.

Bamber, R.N. (2008). *Tanaidaceans (Crustacea: Peracarida: Tanaidacea) from Moreton Bay, Queensland, Australia*. *In*: Davie, P.J.F. & Phillips, J.A. (eds), Proceedings of the Thirteenth International Marine Biological Workshop, The Marine Fauna and Flora of Moreton Bay, Queensland. Memoirs of the Queensland Museum, Nature, 54 (1): 143–217.

Bamber, R.N. & Chatterjee, T. (2010). The new and the old: littoral tanaidomorph Tanaidacea (Crustacea: Peracarida) from the Andaman Islands, Indian Ocean. *Zootaxa*, 2558: 17–32.

Bamber, R.N. & Costa, A.C. (2009). The tanaidaceans (Arthropoda: Peracarida: Tanaidacea) of São Miguel, Azores, with description of two new species, and a new record from Tenerife. *Açoreana*, 6: 183–200.

Barnard, K.H. (1920). Contributions to the crustacean fauna of South Africa. 6. Further additions to the list of marine Isopoda. *Annals of the South African Museum*, 17 (5): 319–438.

Beddard, F.E. (1886). I. Report on the Isopoda collected by H.M.S. 'Challenger' during the years 1873-1876. *Report on the Scientific Results of the Voyage of H.M.S. 'Challenger' During the Years 1873-1876*, Second part, Zoology, 17: 1–178.

Bird, G.J. (2011). Paratanaoidean tanaidaceans (Crustacea: Peracarida) from littoral and shallow sublittoral habitats in New Zealand, with descriptions of three new genera and seven new species. *Zootaxa*, 2891: 1–62.

Bird, G.J. & Bamber, R.N. (2000). *Additions to the tanaidomorph Tanaidacea (Crustacea: Peracarida) of Hong Kong*. Pp. 65–104. *In*: Morton, B. (ed), The Marine Flora and Fauna of Hong Kong and Southern China. V. Proceedings of the Tenth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong, 6–26 April, 1998. Hong Kong, Hong Kong University Press.

Bird, G.J. & Larsen, K. (2009). Tanaidacean phylogeny - the second step: the basal paratanaoidean families (Crustacea: Malacostraca). *Arthropod Systematics and Phylogeny,* 67 (2): 137–158.

Dana, J.D. (1849). Conspectus Crustaceorum. Conspectus of the Crustacea of the U.S. Exploring Expedition. *American Journal of Science and Arts, Series 2*, 8: 424–428.

Dana, J.D. (1852). On the classification of the Crustacea Choristopoda or Tetrapoda. *American Journal of Sciences and Arts*, Series 2, 14: 197–306.

Dojiri, M. & Sieg, J. (1997). *The Tanaidacea*. Pp. 181–278. *In*: Blake, J.A. & Scott, P.H. (eds), Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Volume 11. The Crustacea Part 2. The Isopoda, Cumacea and Tanaidacea. Santa Barbara, CA, Santa Barbara Museum of Natural History.

Gardiner, L.F. (1975). The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea). *Smithsonian Contributions to Zoology,* 170: 1–265.

Guţu, M. (1991). The description of *Paradoxapseudes cubensis*, a new genus and new species of Tanapseudidae (Crustacea, Tanaidacea). *Travaux du Muséum National d´Histoire Naturelle ‘Grigore Antipa*’, 31: 355–364.

Guţu, M. (1996). Tanaidaceans (Crustacea, Peracarida) from Brazil, with descriptions of new taxa and systematical remarks on some families. *Travaux du Muséum National d´Histoire Naturelle ‘Grigore Antipa*’, 35: 23–133.

Guţu, M. (1998). Malacostraca-Peracarida. *Tanaidacea*. Pp. 549–557. *In:* Young, P.S. (ed), Catalogue of Crustacea of Brazil. Rio de Janeiro, Museu Nacional. (Série Livros n° 6).

Guţu, M. (2006). New Apseudomorph Taxa of the World Ocean: Crustacea, Tanaidacea. Curtea Veche, Bucharest, Romania, Pp. 318.

Guţu, M. (2007). Contribution to the knowledge of the Indo-West-Pacific Apseudomorpha (Crustacea: Tanaidacea). *Travaux du Muséum National d´Histoire Naturelle ‘Grigore Antipa’*, 50: 47–86.

Guţu, M. (2008). New data on the genus *Paradoxapseudes* Guţu, 1991, including the description of a new species. The synonymisation of *Gollumudes* Bamber, 2000 with *Paradoxapseudes* and the description of a new apseudid genus. *Travaux du Museum National d’Histoire Naturelle ‘Grigore Antipa’*, 51: 17–42.

Guţu, M. (2009). A contribution to the knowledge of metapseudids. Description of a new genus and three new species from the Caribbean Sea and the Indian Ocean (Crustacea: Tanaidacea: Apseudomorpha). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'*, 52: 101–125.

Guţu, M. & Ramos, G.E. (1995). Tanaidaceans (Crustacea, Peracarida) from the waters of Colombian Pacific with the description of two new species. *Travaux du Muséum National d´Histoire Naturelle 'Grigore Antipa'*, 35: 29–48.

Hansen, H.J. (1895). Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt-Stiftung*, 2: 1–105.

Heard, R.W., Hansknecht, T. & Larsen, K. (2003). An illustrated identification guide to Florida Tanaidacea (Crustacea: Peracarida) occurring in depths of less than 200 m, Pp. 163. State of Florida, Department of Environmental Protection, Tallahassee.

Krøyer, H. (1842). Nye arter af slægten Tanais. *Naturhistorisk Tidskrift*, 4: 167–188.

Kudinova-Pasternak, R.K. (1965). Deep-sea Tanaidacea from the Bougainville Trench of the Pacific. *Crustaceana*, 8 (1): 75–91.

Kudinova-Pasternak, R.K. (1976). Deep sea bottom fauna of the Pacific Ocean. *Academy Sciences of URSS*, 99: 115–125.

Kudinova-Pasternak, R.K. (1977). Tanaidacea (Crustacea, Malacostraca) from the deep sea trenches of the western part of the Pacific. *Transactions of the Institute of Oceanology,* 108: 115–135.

Kudinova-Pasternak, R.K. (1981). Tanaidacea. p. 94–112. *In:* Kusnjezov, A.P. & Mironov, A.N. (eds), Benthos of the submarine mountain Markus Necker and adjacent Pacific regions. (Shirshov Institute of Oceanology, Academy of Science, Moscow).

Kudinova-Pasternak, R.K. (1985). Tanaidacea (Crustacea, Malacostraca) collected on the summit and at foot of Great-Meteor Seamount. *Zoologicheskii Zhurnal*, 120: 52–64.

Kudinova-Pasternak, R.K. (1990). Tanaidacea (Crustacea, Malacostraca) of the underwater ridge Naska in the Pacific. Zoologicheskii Zhurnal, 69 (12): 135–140.

Kussakin, G.O. & Tzareva, L.V. (1972). Tanaidacea from the coastal zones of the middle Kurile Islands. *Crustaceana*, 3: 237–245.

Lang, K. (1949). Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologi*, 42: 1–14.

Lang, K. (1950). The genus Pancolus Richardson and some remarks on *Paratanais euelpis* Barnard (Tanaidacea). *Arkiv för Zoologi*, 2: 357–360.

Lang, K. (1956). Tanaidacea aus Brasilien, gesammelt von Professor Dr. A. Remane und Dr. S. Gerlach. Kieler Meeresforschungen, 12: 249–260.

Lang, K. (1970). Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen 4: Aufteilung der Apseudiden in vier Familien nebst Aufstellung von zwei Gattungen und einer Art der neuen Familie Leiopidae. *Arkiv för Zoologi*, 22: 595–626.

Lang, K. (1973). Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen (Crustacea). 8. Die Gattungen *Leptochelia* Dana, *Paratanais* Dana, *Heterotanais* G.O. Sars und *Nototanais* Richardson. Dazu einige Bemerkungen über die Monokonophora und ein Nachtrag. *Zoologica Scripta*, 2: 197–229.

Larsen, K. (1999). A new species of the deep-sea genus *Carpoapseudes* (Crustacea: Tanaidacea) from southwestern Atlantic. *Zoosystema*, 21: 647–659.

Larsen, K. (2001). Morphological and molecular investigation of polymorphism and cryptic species in tanaid crustaceans: implications for tanaid systematics and biodiversity estimates. *Zoological Journal of the Linnean Society*, 131: 363–379.

Larsen, K. (2003). Proposed new standardized terminology for tanaidacean Crustacea. *Journal of Crustacean Biology*, 23 (3): 644–661.

Larsen, K. (2005). Deep-Sea Tanaidacea (Peracarida) from the Gulf of Mexico. *Crustaceana Monographs* 5, Leiden, Brill, Pp. 387.

Larsen, K., Araújo-Silva, C.L. & Coelho, P.A. (2009). Tanaidacea from Brazil. I. The family Tanaellidae Larsen & Wilson, 2002. *Zootaxa*, 2141: 1–19.

Larsen, K., Nagaoka, R. & Froufe, E. (2012). Tanaidacea (Crustacea) from Macaronesia III. The shallow-water Tanaidomorpha from the Cape Verde archipelago.*Zootaxa*, 3498: 24–44.

Larsen, K. & Shimomura, M. (2007). Tanaidacea (Crustacea: Peracarida) from Japan. II. Tanaidomorpha from the East China Sea, the West Pacific Ocean, and the Nansei Islands. *Zootaxa*, 1464: 1–43.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny, the first step: the superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research*, 40: 205–222.

Larwood, H.J.C. (1940). The fishery grounds near Alexandria, XXI. Tanaidacea and Isopoda. Fouad I Institute of Hydrobiology and Fisheries, Notes and Memoires, 35: 1–72.

Leach, W.E. (1814). *Crustaceology*. Pp. 383–437. *In*: Brewster, D. (ed), The Edinburgh Encyclopedia, Edinburgh.

Makkaveeva, E.B. (1971). Kachestvenniy sostav i kolichestvennoe raspredelinie tanaidovikh rakov v Krasnom More [Qualitative composition and quantitative distribution of tanaidacean crustaceans in the Red Sea]. p. 88-108. *In:* Anonymous (ed), Bentos Shelfa Krasnogo Morya [Shelf Benthos of the Red Sea]. Kiev, Naukova Dumka.

Mañé-Garzón, F. (1949). Un nuevo tanaidaceo ciego de Sud America, *Kalliapseudes schubartii*, nov. sp. *Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo*, 52 (3): 1–6.

Masunari, S. & Sieg, J. (1980). Morphological and ecological notes on *Zeuxo coralensis* Sieg, 1980 from Brazil. *Studies on Neotropical Fauna and Environment*, 15: 1–8.

Monod, T. (1925). Tanaidacés et Isopodes aquatiques de l’Afrique occidentale et septentrionale. (1re partie: Tanaidacea, Anthuridea, Valvifera). *Bulletin de la Société des Sciences Naturelles du Maroc*, 3 (1): 61–77.

Rapoport, E.H. (1982). Areography: geographical strategies of species. Pergamon Press, Oxford, 269p.

Santos, K.C. (2007). Three new species of *Kudinopasternakia* Guţu, 1991 (Crustacea: Tanaidacea: Sphyrapodidae) from Brazilian waters. *Zootaxa*, 1666: 23–41.

Santos, K.C. & Hansknecht, T. (2007). *Taraxapseudes* n. gen., *Taraxapseudes diversus* (Lang, 1968) n. comb. and two new species of *Atlantapseudes* Băcescu, 1978 (Tanaidacea: Apseudidae) from Brazil and Madagascar, with a key for the genus. *Zootaxa*, 1639: 23–39.

Santos, K.C. & Pires-Vanin, A.M.S. (2006). Redescription of *Parapagurapseudopsis carinatus* (Tanaidacea: Apseudomorpha) and remarks about the male form. *Zootaxa*, 1363: 39–48.

Santos, K.C., Santana, W. & Pires-Vanin, A.M.S. (2012). *Postispinatus youngi* n. gen., n. sp. (Apseudomorpha; Tanaidacea; Crustacea): phylogenetic analysis and taxonomic remarks about kalliapseudids. *Zootaxa*, 3192: 24–38.

Shiino, S.M. (1978) (published 1979). Tanaidacea collected by French Scientists on board the survey ship 'Marion-Dufresne' in the regions around the Kerguelen Islands and other subantarctic islands in 1972, '74, '75, '76. *Science Report of Shima Marineland*, 5: 1–122.

Sieg, J. (1976). Zum natürlichen System der Dikonophora Lang (Crustacea, Tanaidacea). Zeitschrift für zoologischer Systematik und Evolutions forschung, 14: 177–198.

Sieg, J. (1980a). Taxonomische Monographie der Tanaidae Dana, 1849 (Crustacea: Tanaidacea). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 537: 1–267.

Sieg, J. (1980b). Sind die Dikonophora eine polyphyletische Gruppe? Zoologischer Anzeiger, 205: 401–416.

Sieg, J. (1981). A new species of the genus *Paratanais* (Crustacea: Tanaidacea), *P. spinanotandus*, from Seamount Vema. *Proceedings of the Biological Society of Washington,* 94 (4): 1271–1278.

Sieg, J. (1983). Contribution to the knowledge of the Tanaidacea (Crustacea) of Brazil. 1. The family Tanaidae Dana, 1849. *Papéis Avulsos de Zoologia*, São Paulo, 35 (3): 31–39.

Sieg, J. (1986). Crustacea Tanaidacea of the Antarctic and the Subantarctic. 1. On material collected at Tierra del Fuego, Isla de los Estados, and the west coast of the Antarctic Peninsula. p. 1-180. In: Korniker, L.S. (ed), Biology of the Antarctic Seas 18. Volume 45 in the Antarctic Research Series. Washington, D.C., American Geophysical Union.

Sieg, J. & Dojiri, M. (1989). Remarks on *Araphura* Bird and Holdich (Crustacea, Tanaidacea) and allied genera, including descriptions of three new species. *Zoologica Scripta*, 18: 115–137.

Sieg, J. & Heard, R.W. (1985). Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico. IV. On *Nototanoides trifurcatus* gen. nov., sp. nov., with a key to the genera of the Nototanaidae. *Gulf Research Reports*, 8 (1): 51–62.

Silva-Brum, I.N. (1969). Ocorrência de '*Apseudes intermedius'* Hansen, 1985 e '*Tanais cavolinii'* Milne Edwards, 1829, no litoral Brasileiro (Crustacea, Tanaidacea). *Revista Brasileira de Biologia*, 29: 601–605.

Silva-Brum, I.N. (1971). *Apseudes paulensis* nova espécie de Tanaidacea do litoral Brasileiro (Crustacea). *Arquivos do Museu Nacional,* Rio de Janeiro, 54: 9–14.

Silva-Brum, I.N. (1973). Contribuição ao conhecimento da fauna do Arquipélago de Abrolhos, Bahia, Brasil. Crustacea - Tanaidacea. *Boletim do Museu de História Natural da Universidade Federal de Minas Gerais*, *Zoologia*, 18 (4): 1–25.

Silva-Brum, I.N. (1974). Contribuição ao conhecimento da fauna do Arquipélago de Abrolhos, Bahia, Brasil. Crustacea - Tanaidacea. *Boletim do Museu de História Natural da Universidade Federal de Minas Gerais, Zoologia*, 20 (5): 1–10.

Silva-Brum, I.N. (1978). *Paraleiopus macrochelis* g. n., sp. n. do litoral Sudeste do Brasil (Tanaidacea, Monokophora). *Revista Brasileira de Biologia*, 38 (3): 639–645.

Stebbing, T.R.R. (1896). A new West-Indian tanaid. *Annals and Magazine of Natural History, Series 6*, 17 (97): 49–53.

Vanhöffen, E. (1914). Die Isopoden der deutschen Südpolar Expedition 1901-1903. *Deutsche Südpolar-Expedition, Zoologie*, 15 (7): 447–598.

http://dx.doi.org/10.1590/S0104-64972012000200002.

ISSN 0104-6497

Zootaxa, 3523: 1–19 (2012)

Article 2. Tanaidacea (Tanaidacea: Crustacea) from Brazil. IV. A new genus and two new species from the family Leptocheliidae

Catarina L. Araújo-Silva[1] & Kim Larsen[1]

[1]Laboratory for Marine Community Ecology and Evolution, CIIMAR (Centro Interdisciplinar de Investigação Marinha e Ambiental), University of Porto, Rua dos Bragas, 289, 4050–123 Porto, Portugal (present address). Capes Foundation, Ministry of Education of Brazil, Brasília–DF, 70040–020, Brazil. E-mail: katelas@hotmail.com; tanaids@hotmail.com

Abstract

This study is based on the material collected from REVIZEE Program and under the Petrobrás oil-exploration programs. These collections revealed a number of representatives from the family Leptocheliidae in its broadest sense, with descriptions of one new genus, *Makraleptochelia* n. gen., and two new species, *M. potiguara* n. sp. and *Intermedichelia jesseri* n. sp. The new genus appears to be closely related to *Konarus-Parakonarus-Pseudoleptochelia* complex of species and differs mainly in the extremely elongated habitus of the male. *Intermedichelia jesseri* is only the second recorded species of this genus and is separated from the other species by having two distal simple setae on the lateral projections of pereonite 3, two distal simple setae on the maxilliped basis, one ventrodistal spiniform seta on the merus-carpus-propodus of pereopod 3, and pereopods 4 and 5 propodus with one dorsodistal simple seta marginally longer than dactylus and unguis combined. *Intermedichelia* is here included in the family Leptocheliidae.

Key words: Crustaceans, Tanaidaceans, REVIZEE Program, Leptocheliidae, *Makraleptochelia*, *Intermedichelia*, northeastern coast of Brazil

Introduction

This is the fourth study on tanaidacean systematics from Brazil and the second of a series of papers from the northeastern coast of Brazil based on material collected from the REVIZEE Program and also under the Petrobrás oil-exploration programs. For an overview of the earlier literature of the Petrobrás oil-exploration programs and for details on REVIZEE Program see Larsen *et al*. (2009) and Araújo-Silva & Larsen (2013), respectively.

The family Leptocheliidae Lang, 1973 is well represented in Brazilian waters (Krøyer 1842; Dana 1849; Silva-Brum 1973; Masunari 1983; Guţu 1996, 1998), including three of the earliest-described species of the family collected, *Leptochelia dubia* (Krøyer, 1842), *L. brasiliensis* (Dana, 1849), *L. forresti* (Stebbing 1896), and the more recent *Intermedichelia gracilis* Guţu, 1996 which is mainly distinguished by the expanded projections on the medial margins of pereonite 3.

The species described in this paper are all ‘leptochelids’, although the family Leptocheliidae is rather poorly defined (Bird & Larsen 2009) and currently undergoing revision (Bird pers. comm.) the family designation chosen here is thus in its broadest sense (Lang 1973). An example is the genus *Intermedichelia* Guţu, 1996, considered genus *incertae sedis* by Bird & Larsen (2009) mainly owing to the character of the modified propodal dorsodistal seta of pereopods 4–5 (Bird & Larsen 2009:148[94]); previously, Larsen & Wilson (2002) included this genus in the subfamily Leptocheliinae Lang, 1973. The present study describes a new species with expanded diagnostic characters for *Intermedichelia* and could potentially resolve its systematics position. The genus is considered endemic for Brazilian waters; *I. gracilis* was collected in Rio de Janeiro (type-locality) and recently Araújo-Silva & Larsen (2012) registered the first occurrence for the northeastern coast of Brazil.

The new genus appears to be closely related to the females of *Pseudoleptochelia* Lang, 1973, *Konarus* Bamber, 2006 and *Parakonarus* Bird, 2011, and due to the subchelate cheliped of the male (although males are unknown for *Konarus*), but differs mainly in the extremely elongated habitus of the male which was never previously recorded in the Leptocheliidae (see generic remarks of the genus).

Material and methods

Specimens were collected from the continental shelf within the Exclusive Economic Zone of Brazil, between Foz do Rio Parnaíba (Piauí State [PI]) and Salvador (Bahia State [BA]). Most of the material was collected with Dredge (70 L) by the Brazilian navy RV Antares (Directorate of Hydrography and Navigation) on the expeditions Northeast I (NE I) (1995), III (NE III) (1998) and IV (NE IV) (2000) during the 'Programa de Avaliação do Potencial Sustentável dos Recursos Vivos na Zona Econômica e Exclusiva do Brasil' (REVIZEE Program) and other part collected with a Van Veen Grab (230 L) by the navy RB Seward Johnson on the expedition PAI (2009), during 'Programa de Avaliação da Biota Bentônica e Planctônica das Bacias Potiguar e Ceará.'

Body length was measured from the anterior margin of the carapace rostrum to the tip of the telson in lateral view to avoid bias from a flexed body posture. Body width was measured on the widest part of the carapace in dorsal view. Terminology follows Larsen (2003). Adjectives such as long and short are used as relative qualifiers in respect of the appendage/structure being described. Dissections were made with chemically-sharpened tungsten wire needles. Whole animal illustrations were made from type specimens while appendages were dissected and drawn from paratypes. Type material is kept at the Carcinological Collection of the Museu de Oceanografia Petrônio Alves Coelho da Universidade Federal de Pernambuco (MOUFPE).

Systematics

Order Tanaidacea Dana, 1849

Suborder Tanaidomorpha Sieg, 1980

Family Leptocheliidae Lang, 1973

Genus *Makraleptochelia* **n. gen**.

Diagnosis. **Female**. Body robust. Carapace dorsal suture absent, about five to six times as long as wide. Eyes present. Pereonites 4 and 5 longest. Antennule with four articles (terminal article reduced); proximal article stout, about 1.8 times as long as wide. Antenna without distal spiniform setae on articles 2 or 3. Maxilliped endite with three distal spiniform complex setae; basis with six distal simple setae.

Cheliped sclerite with three proximal simple setae; basis with one specialized seta arising from sub-dorsodistal tubercle; merus with 13–14 ventral simple setae; carpus outer ventrodistal margin extended as a 'shield' overlapping propodus. Pereopodal ischia with two simple setae. Pereopod 1 unguis about 1.6 times as long as dactylus. Pereopods 4–6 unguis incompletely fused with dactylus. Pleopod basal article short and naked. Uropod endopod with four articles; exopod uniarticulate. **Male:** body extremely elongate, about 18.5 times as long as wide. Cephalothorax with eight short simple setae on lateral margins, eyes present. Pereon naked, about 15 times as long as wide. Pleon short, about 10% of total body length. Antennule with multiple serially repeating articles densely covered with aesthetascs ventrally. Antenna of six articles (terminal article reduced). Maxilliped basis with six–seven distal simple setae; palp naked, biarticulate. Epignath elongate, naked. Cheliped sclerite with three proximal simple setae; merus with 13–14 simple ventral setae; carpus robust, outer ventrodistal margin slightly covering proximal part of propodus; propodus subchelate; dactylus with five short spiniform setae on inner margin. Pereopods 1–6 ischia with two ventral simple setae. Pleopods with basal article naked. Uropod endopod of three articles; exopod of one article.

Type species. *Makraleptochelia potiguara* n. sp.

Gender. Feminine.

Etymology. The genus is derived from Greek *Makra* = long, + *Leptochelia*, due the elongate body of the male.

Generic remarks. *Makraleptochelia* is mainly separated from other genera by the extremely elongate body shape of the male; despite the female of *Makraleptochelia* sharing a combination of characters with species of *Konarus* and *Parakonarus*, which suggest that this species could be a 'link' between these two genera, they can be separated by having: 1) the carapace dorsal suture absent (present in both *Parakonarus* and *Konarus*); 2) the six simple setae on anterolateral margins of cephalothorax (naked, or with two to three in *Konarus* and *Parakonarus*); 3) the maxilliped basis with six (six-seven in males) distal simple setae (five or four in *Parakonarus* and *Konarus*); 4) the cheliped merus with at least 13 simple setae (eight to 11 in *Konarus* and *Parakonarus*); 5) the uropod endopod with four articles (five or six in *Parakonarus* and six in *Konarus*); also the male cheliped propodus with more than 20 inner distal spiniform setae (less than 20 spiniform setae in *Parakonarus*), and the pereopod 1 merus with one spiniform seta (one simple seta in *Parakonarus*).

Pseudoleptochelia also have a subchelate male cheliped and no dorsal suture on the female carapace; however, they can be easily separated by *Pseudoleptochelia* species having only few setae on the cheliped merus and the antenna articles 2 and 3 with spiniform setae on distal margins, as well as other characters.

The presence of six (or six–seven in male) simple setae on the maxilliped basis of *M. potiguara* n. sp. is rare in the family Leptocheliidae, and has only been reported for the females of *Leptochelia bispinosa* Guţu, 2011a and *Neoleptochelia javanensis* Guţu, 2011b, the former also showed variation in the setal number between the two endites.

Makraleptochelia potiguara **n. sp.**

(Figures 12–17)

Material examined. Holotype: female with oostegites (REG# MOUFPE 14.370), body length 4.4 mm. Station NE IV #141 (04°91'S 035°22'W). Type-locality: Rio Grande do Norte State [RN], Brazil. Depth: 43 m, 22 November 2000. Allotype: adult male (REG# MOUFPE 14.851), body length 12.5 mm. Station PAI #081 CES 32 R3 (0–10 cm) (03°00'S 038°51'W). Locality: Ceará State [CE], Brazil. Depth: 58 m, 8 July 2009.

Paratypes: one female with oostegites (dissected) (REG# MOUFPE 15.068), and two females without oostegites (REG# MOUFPE 14.371), same locality as holotype. One female without oostegites (REG# MOUFPE 14.372); station NE III #180 (011°55'S 037°23'W), 19 July 1998. Four females without oostegites (REG# MOUFPE 14.373); station NE I #243 (09°17'S 034°91'W), 24 October 1995. One female without oostegites (REG# MOUFPE 14.374); station NE IV #131 (02°23'S 039°89'W), 20 November 2000. One female without oostegites (damaged), (REG# MOUFPE 14.375); station NE IV #165 (08°13'S 034°63'W), 1 December 2000. Two females without oostegites (damaged), (REG# MOUFPE 14.376); station NE IV #178 (011°27'S 037°02'W), 3 December 2000.

Specimens were collected in sandy sediments, sorted from algae and sponges; between 37–71.6 m depth. Locality: Ceará to Bahia State [BA], Brazil.

Etymology. The name reflects the native people in the state of Rio Grande do Norte, “potiguar”, where the holotype was collected.

Description. Based on holotype (4.4 mm) and paratype, female with oostegites.

Body (Figure 12A, B): dorsoventrally flattened, about 5.5 times as long as wide. Cephalothorax: about 1.1 times as long as wide, about 1.5 times as long as two first pereonites combined, six simple setae on each anterolateral margin. Rostrum rounded. Ocular lobes triangular with visual elements. Carapace dorsal suture absent. Pereon: about 3.7 times as long as wide and about 60% of total body length. Pereonites 1 and 2 subequal length, except for pereonite 1 with two pairs of simple setae on each antero- and posterolateral margin. Pereonites 3 and 6 of subequal length, except for pereonite 6 with three simple setae on each anterolateral margin and one simple setae on dorsal margin. Pereonites 4 and 5 longest, with three simple setae on each anterolateral margin and one simple seta on dorsal margin. Pleon: broader than cephalothorax and pereon, about 1.1 times as wide as long, about 21% of total body length. Pleonites subequal with one simple seta on each lateral margin. Pleotelson about 2.2 times as wide as long, with one simple and one setulated seta on dorsomedial margin and two pairs of terminal simple setae.

Antennule (Figure 13H): of four articles (terminal article reduced), about 0.7 times as long as cephalothorax. Article 1 stout, about 1.8 times as long as wide and 1.6 times as long as two following articles, with two simple and several setulated setae on dorsal margin, one medial simple seta on ventral margin. Article 2 about 1.2 times as long as wide, a row of distal fine setules, one simple seta on dorsodistal margin, one setulated and one simple seta on ventrodistal margin. Article 3 as long as article 2, with two distal simple setae. Terminal article with five simple setae, one setulated and one aesthetasc.

Antenna (Figure 13I): of six articles (terminal article reduced), about 0.7 times as long as antennule. Article 1 naked, as long as article 2. Article 2 with two dorsodistal simple setae and one ventrodistal simple seta, dorsal margin with large process and bearing a row of short spines. Article 3 shortest, with three simple setae on dorsodistal margin. Article 4 as long as two first articles combined, ventrodistal margin with one pair of simple and setulated setae, dorsomedial margin with subdistal scales, one simple and one setulated seta, dorsodistal margin with one setulated and one simple seta. Article 5 with two distal simple setae and one setulated seta. Terminal article with five simple setae.

Mouthparts (Figure 13A–F): labrum (Figure 13A) rounded with several fine setules on distal and lateral margins. Mandibles (Figure 13B, C) molar process broad with serrate edges. Left mandible (Figure 13B) lacinia mobilis slightly longer than incisor, with apparently five denticles on distal margin, incisor crenulate. Right mandible (Figure 13C) incisor crenulate with several denticles on distal margin. Labium (Figure 13D) with two pairs of lobes, distal margins with several setae. Maxillule (Figure 13E) palp not recovered; endite with several fine setules on lateral margins, 12 distal spiniform setae. Maxilla not recovered. Maxilliped (Figure 13F) endite with several fine setules on outer distal margin, three complex setae and one denticle on inner distal margin; basis about twice as long as wide, with six distal simple setae. Palp article 1 naked, about 1.3 times as long as article 2; article 2 with one simple seta on outer distal margin, five simple setae on inner distal margin; article 3 longest, about 1.2 times as long as article 1, with five simple and three serrated setae on inner margin; article 4 with two simple and nine serrated setae on inner margin. Epignath not recovered.

Cheliped (Figure 12C): attached via sclerite, with three proximal simple setae. Basis about 1.7 times as long as wide, with one dorsodistal seta mounted on tubercle. Merus triangular with 14 ventral simple setae. Carpus stout, about 1.6 times as long as wide, carpus outer ventrodistal margin extended as ‘shield’ overlapping propodus, slightly longer than basis, with four dorsoproximal short simple setae and one simple on dorsodistal margin, three ventromedial simple setae. Propodus about 1.6 times as long as wide, with several fine simple setules, six inner bipinnate setae on dorsal margin and one ‘S’ shaped simple seta next to insertion of dactylus. Fixed finger with carina and three simple setae on inner margin, two ventral simple setae. Dactylus and unguis naked.

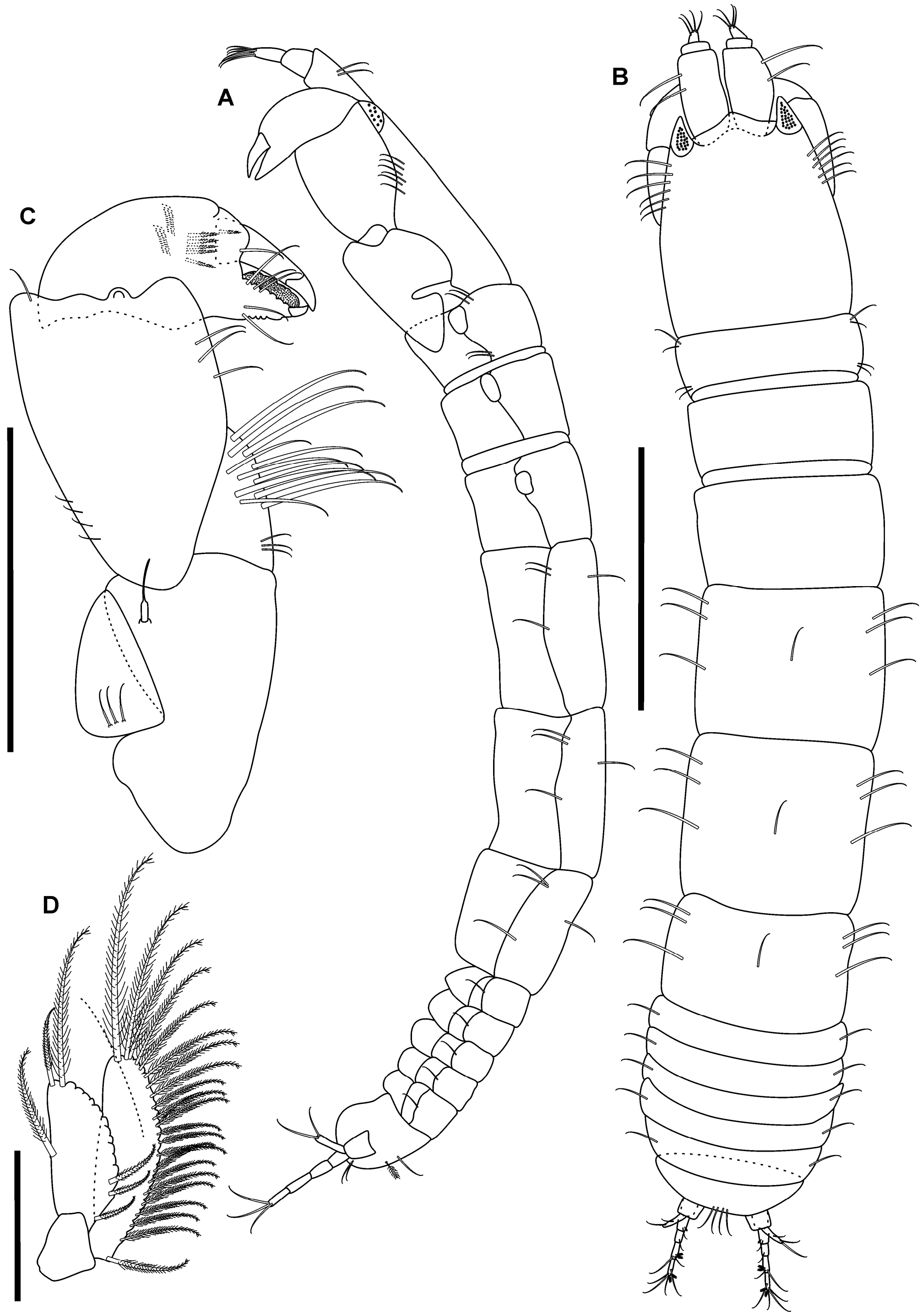


Figure 12. *Makraleptochelia potiguara* n. sp., female, holotype. (A) Lateral view; (B) dorsal view. Paratype, female: (C) cheliped; (D) pleopod. (A–B) Scale bar = 1 mm; (C) scale bar = 0.5 mm and (D) scale bar = 0.2 mm.

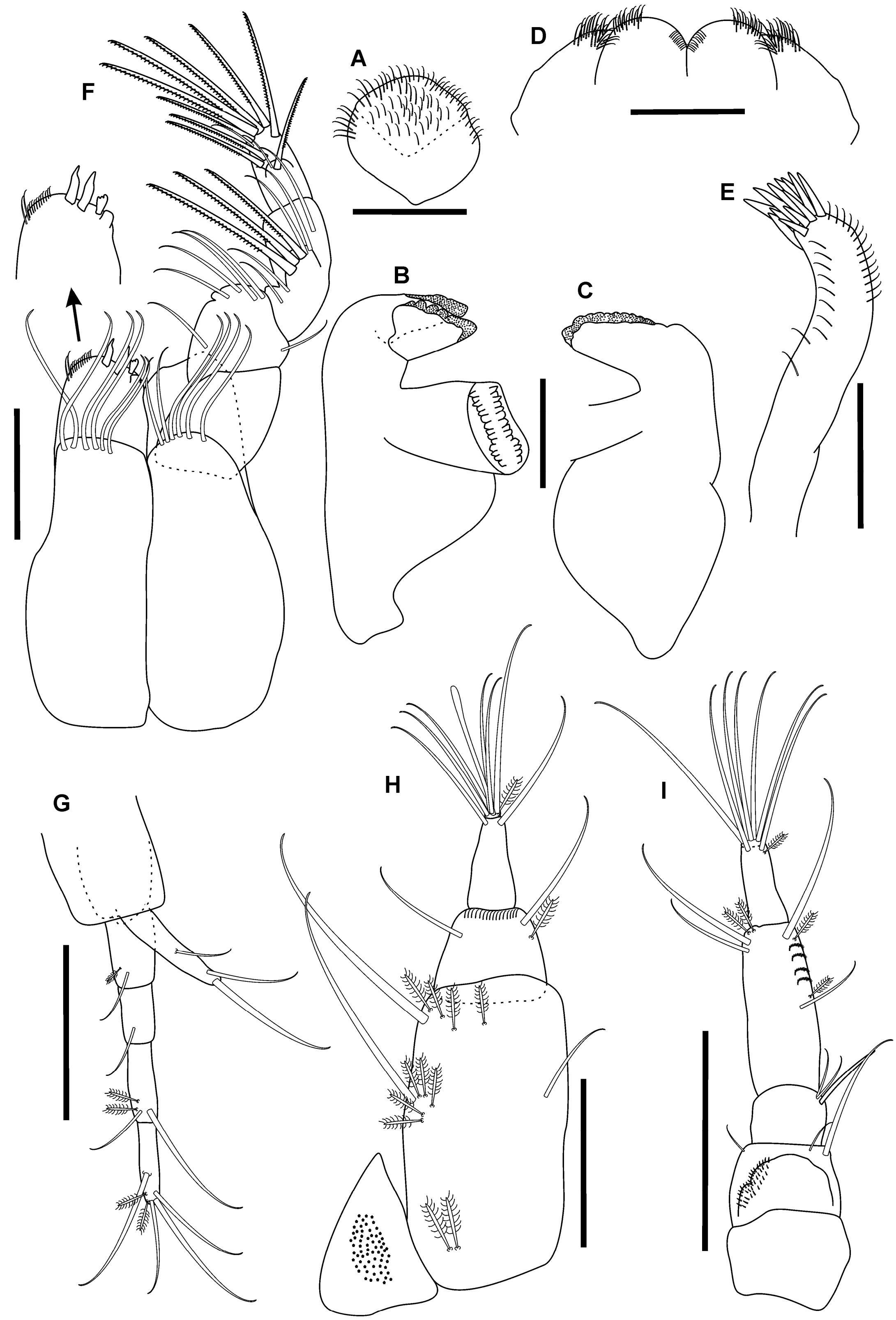


Figure 13. *Makraleptochelia potiguara* n. sp., female, paratype. (A) labrum; (B) left mandible; (C) right mandible; (D) labium; (E) maxillule; (F) maxilliped; (G) uropod; (H) antennule; (I) antenna. (A–F) Scale bars = 0.1 mm and (G–I) 0.2 mm.

Pereopod 1 (Figure 14A): longer and slender than other pereopods. Coxa with one simple seta. Basis about four times as long as wide, with one simple seta and one setulated seta on dorsoproximal margin. Ischium with two ventral simple setae. Merus about 3.4 times as long as wide, with one ventrodistal simple seta. Carpus as long as merus, with two dorsodistal simple setae and three simple on ventrodistal margin. Propodus as long as carpus, with scales on dorsal margin, with four simple and two bipinnate setae on dorsodistal margin, one ventrodistal simple seta. Dactylus and unguis combined about 1.5 times as long as propodus. Unguis about 60% of combined dactylus and unguis length.

Pereopod 2 (Figure 14B): coxa as pereopod 1. Basis about three times as long as wide, with one simple seta and two dorsomedial setulated setae. Ischium as pereopod 1. Merus about 1.8 times as long as wide, with fine simple setules on ventrodistal margin. Carpus slightly shorter than merus, with one dorsodistal simple seta, fine setules and two simple setae on ventrodistal margin. Propodus about 2.8 times as long as wide and 1.5 times as long as dactylus and unguis combined, with scales on dorsal margin, a row of ventral short spines, one simple seta, dorsodistal margin with one bipinnate seta and one short spiniform seta, ventrodistal margin with one pair of simple setae, one spiniform seta and another pair of bipinnate setae. Dactylus and unguis combined about 0.4 times as long as dactylus/unguis of pereopod 1. Unguis as long as dactylus.

Pereopod 3 (Figure 14C): as pereopod 2 except carpus with one pair of simple setae on each distal margin. Propodus about 2.3 times as long as wide.

Pereopod 4 (Figure 14D): no visible coxa. Basis stout, about 1.5 times as long as wide, with three dorsomedial setulated setae and another two setulated on ventromedial. Ischium with two ventral simple setae. Merus about twice as long as wide, with several scales, and two spiniform setae with medial ring of spinules on ventrodistal margin. Carpus robust, about 1.3 times as long as wide and about 1.2 times as long as merus, with several ventral scales and fine simple setules, and three ventrodistal spiniform setae. Propodus slightly longer than carpus, with scales and fine simple setules on ventral margin, two ventrodistal spiniform setae, dorsodistal margin with one pair of serrated setae and another pair of bipinnate setae. Dactylus with one dorsoproximal simple seta. Unguis incompletely fused with dactylus.

Pereopod 5 (Figure 14E): as pereopod 4 except merus with two ventrodistal spiniform setae. Carpus with two dorsodistal simple setae and two ventrodistal spiniform setae with medial ring of spinules. Propodus with one short spiniform seta and three serrated setae on dorsodistal margin, and two circumplumose spiniform setae on ventrodistal margin.

Pereopod 6 (Figure 14F): as pereopod 5 except basis about 1.7 times as long as wide, with one dorsomedial simple seta. Carpus with one dorsodistal simple seta. Propodus with six dorsodistal serrated setae and two ventrodistal spiniform setae.

Pleopods (Figure 12D): basal article short and naked. Exopod with 22 plumose setae. Endopod with one outer and 17 inner plumose setae, distal seta with serrated apex.

Uropod (Figure 13G): basal article naked. Endopod of four articles; article 1 with one simple and one setulated seta; article 2 with one simple seta; article 3 with one pair of setulated and another pair of simple setae; article 4 with two setulated and four simple setae. Exopod uniarticulate, about 1.6 times as long as first endopod article, with one medial and two distal simple setae.

Description of male allotype: adult of 12.5 mm (partly dissected).

Body (Figure 15A, B): dorsoventrally flattened, slender and about 18.5 times as long as wide. Cephalothorax: about twice as long as wide and 1.4 times as long as pereonite 1. Widest at mid-length. Rostrum pronounced and tapering into a blunt apex. Triangular eye-lobes and visual elements present. With eight short simple setae on each lateral margin. Pereon: naked, extremely elongate, about 15 times as long as wide and 80% of total body length. Pereonites 1–3 not reduced. Pereonite 1 shorter than other pereonites, about 1.5 times as long as wide. Pereonites 2 and 6 subequal, about 1.5 times as long as pereonite 1 and shorter than pereonites 3–5. Pereonites 3 and 4 subequal. Pereonite 5 longest, about 4.2 times as long as wide. Pleon: naked, about 1.7 times as long as wide and 10% of total body length. Pleonites short, about four times as wide as long. Pleotelson about twice as wide as long, with two dorsal setulated setae and two pairs of terminal simple setae.

Antennule (Figure 16A): of 13 articles. Article 1 about twice as long as wide and about 0.3 times as long as cephalothorax, with two dorsomedial setulated setae, ventrodistal margin with five setulated and two simple setae. Article 2 about 1.6 times as long as wide and 0.8 times as long as article 1, ventrodistal margin with one simple seta and three setulated setae. Article 3 bearing covering first of serially repeating articles with one dorsodistal simple seta and and several aesthetascs on ventrodistal margin, also with process bearing one dorsodistal simple seta and ventrodistal aesthetascs. Serially repeating articles subequal with a row of ventrodistal aesthetascs. Terminal article with five simple setae, two setulated and four aesthetascs.

Antenna (Figure 16B): of six articles (terminal article minute), as long as two first antennule articles. Article 1 naked. Article 2 dorsal margin with process and bearing a row of short spines and fine simple setae, with one dorsodistal simple seta, ventrodistal margin with one spiniform and one simple seta. Article 3 with one dorsodistal simple seta. Article 4 longest, about 3.2 times as long as wide, slightly shorter than articles 1–3 combined, with one dorsomedial simple seta, ventral margin with three medial setulated setae, three simple and three setulated setae distally. Article 5 about 0.5 times as long as article 4, with two ventrodistal simple setae. Terminal article with six simple setae.

Mouthparts (Figure 16C, D): labrum, mandibles and labium reduced. Maxilliped (Figure 16C) basis robust, longer than wide, distal margin with six long setae on one endite and seven on the other. Palp biarticulate, both naked. Epignath (Figure 16D) elongate, naked.

Cheliped (Figure 15C): attached via sclerite, with three proximal simple setae. Basis stout, 2.1 times as long as wide, with one dorsodistal simple seta. Merus triangular, with 13 ventral simple setae. Carpus stout, about 1.3 times as long as wide, outer ventrodistal margin slightly extended as ‘shield’ overlapping propodus, dorsal margin with four medial simple setae and one simple distally, three ventromedial simple setae. Propodus about 2.1 times as long as wide, slightly longer than carpus, with a row of inner distal spiniform setae (≈ 26) and one dorsodistal ‘S’ shaped simple seta next to dactylus insertion. Fixed finger short, with two ventral simple setae and three simple on inner margin. Dactylus about three times as long as fixed finger, with five inner denticles; i.e. cheliped of subchelate form.

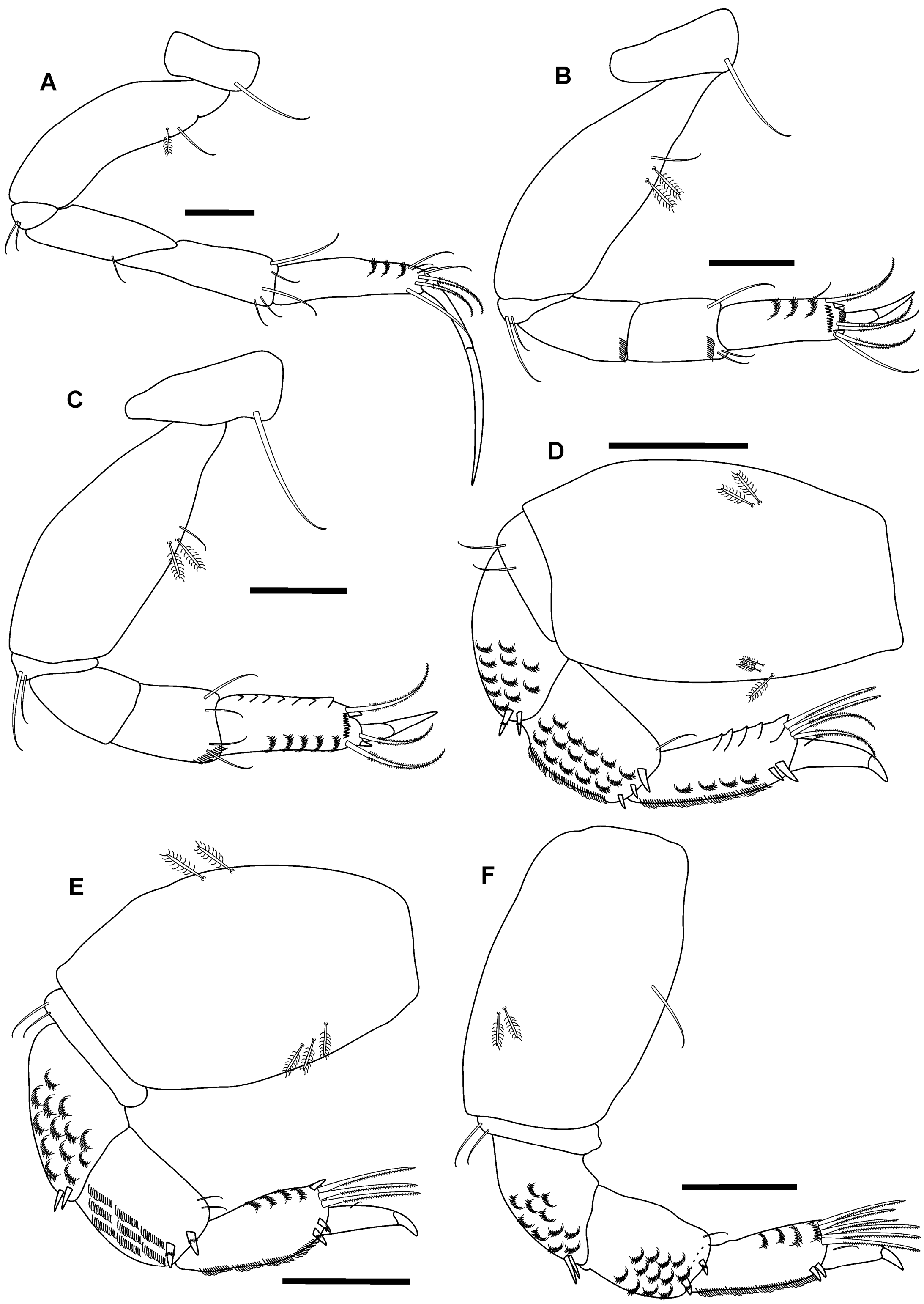


Figure 14. *Makraleptochelia potiguara* n. sp., female, paratype. (A) Pereopod 1; (B) pereopod 2; (C) pereopod 3; (D) pereopod 4; (E) pereopod 5; (F) pereopod 6. (A–F) Scale bars = 0.2 mm.

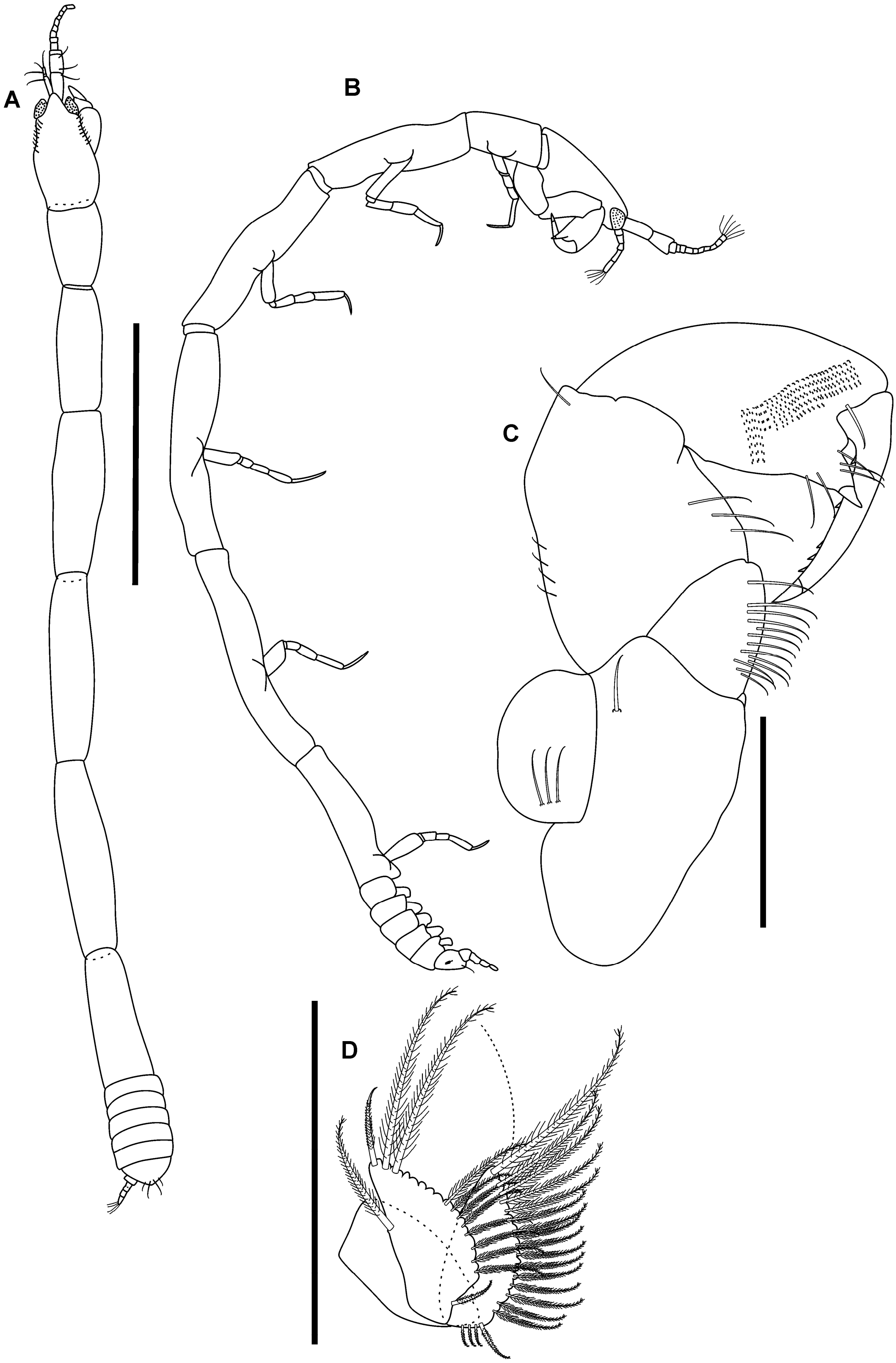


Figure 15. *Makraleptochelia potiguara* n. sp., male, allotype. (A) Dorsal view; (B) lateral view; (C) cheliped; (D) pleopod. Scale bars (A–B) = 3 mm and scale bar (C–D) = 0.5 mm.

Pereopod 1 (Figure 16F): coxa with one simple seta. Basis about 3.8 times as long as wide, with two ventroproximal setulated setae. Ischium with two ventral simple setae. Merus about 3.3 times as long as wide, with one ventrodistal spiniform seta. Carpus as long as merus, with three simple setae and one spiniform seta on dorsodistal margin, ventrodistal margin with one bipinnate seta and two simple setae. Propodus longer than carpus, about 5.7 times as long as wide, with scales on each margin, with three dorsodistal simple setae and one ventrodistal spiniform seta. Dactylus and unguis combined about 0.7 times as long as propodus, dactylus with short spines on proximal margin. Unguis as long as dactylus.

Pereopod 2 (Figure 16G): as pereopod 1 except basis slightly shorter, about 3.3 times as long as wide, with three setulated setae and one simple seta on dorsoproximal margin. Merus with scales and one spiniform seta on dorsodistal margin. Carpus with scales on each lateral margin, with one dorsodistal spiniform seta, ventrodistal margin with one simple seta and two spiniform setae. Dactylus and unguis combined about 0.5 times as long as propodus, with fine simple setules. Unguis about 0.8 times as long as dactylus.

Pereopod 3 (Figure 17A): as pereopod 2 except basis with one simple and one setulated seta on dorsoproximal margin. Merus with one ventrodistal spiniform seta.

Pereopod 4 (Figure 17B): no visible coxa. Basis about twice as long as wide, with three dorsoproximal setulated setae and one ventromedial setulated seta. Ischium with two ventral simple setae. Merus about 2.3 times as long as wide, with fine distal simple setules on ventral margin. Carpus as long as merus, with fine distal simple setules, two dorsodistal simple setae, ventrodistal margin with three serrated spiniform setae and one simple seta. Propodus about 6.5 times as long as wide and slightly shorter than basis, with several short spines on subdistal margin, four dorsodistal simple setae, two ventrodistal spiniform setae. Dactylus about 80% of total dactylus and unguis combined length, with short spines on all ventral margin. Unguis minute.

Pereopod 5 (Figure 17C): as pereopod 4 except basis with four dorsoproximal setulated setae, two ventromedial setulated setae. Merus with two ventrodistal circumplumose spiniform setae and scales. Carpus with three dorsodistal simple setae. Propodus with three dorsodistal simple setae and two ventrodistal serrated setae. Dactylus with three ventrodistal simple setules.

Pereopod 6 (Figure 17D): as pereopod 5 except basis about 2.5 times as long as wide, with three dorsoproximal setulated setae and one ventromedial simple seta. Merus with two ventrodistal serrated spiniform setae. Carpus with two ventrodistal serrated spiniform setae. Propodus about 5.6 times as long as wide, with four dorsodistal serrated spiniform setae and two spiniform setae on ventrodistal margin. Dactylus slightly shorter than pereopods 4–5.

Pleopods (Figure 15D): basal article naked. Exopod with 20 plumose setae. Endopod with one outer medial seta and 16 plumose setae on inner margin, distal seta with serrated apex.

Uropod (Figure 16E): basal article with four simple setae and one setulated seta. Endopod of three articles; article 1 with fusion line, three simple and two setulated setae on medial margin, three simple setae and one setulated seta distally; article 2 with two simple and two setulated setae; article 3 with fusion line, five simple setae and one setulated seta. Exopod uniarticulate with fusion line, 0.7 times as long as endopod article 1, with three simple setae.

Geographical distribution. Type material was found with a large distribution range on the northeastern coast of Brazil, from Ceará [CE] to Bahia State [BA].

Remarks. Recently, Edgar (2012) described *Parakonarus robertsoni* collected on Seven Mile Beach, Australia, which has close affinities to the female of *M. potiguara* in having a cheliped merus with about 11 ventral simple setae (13–14 in *M. potiguara*), four distal simple setae on maxilliped basis (six in *M. potiguara*), pereopods 1–3 ischia with one ventral simple seta (in *M. potiguara* all pereopod ischia with two ventral simple setae), uropod endopod with six articles (four in *M. potiguara*).

Even though the female and male was collected in different stations and years, they overlap the same distribution on northeastern coast of Brazil and share many morphological similarities as the: cephalothorax setae, lack of antennal spiniform setae, setae number of the 1) maxillipedal basis, 2) cheliped sclerite, basis, merus, and carpus, 3) pereopodal ischium. These characters convince us that the male and female are of the same species.

Although the males of *Konarus* species are unknown and therefore cannot be compared and the females morphologically are similar to *Makraleptochelia*, it seems that *Konarus–Parakonarus* group is restricted to Indo-Pacific waters. Therefore, in addition of the morphologic differences described above, we are convinced that these are separate genera.

Genus *Intermedichelia* Guţu, 1996

Diagnosis. Female (modified from Guţu 1996). Body slender, about seven or eight times as long as wide, with an acute lateral prolongation on pereonite 3 with one or two distal simple setae. Cephalothorax as long as two first pereonites combined. Eyes present. Antennule with four articles (terminal article reduced), article 1 longest. Antenna with six articles (terminal article reduced); article 2 with one spiniform seta on dorsodistal margin; article 3 with one distal simple seta. Mandible with strong molar process with numerous notches on masticatory margin. Maxilliped basis with two or three distal simple setae; endite with two flattened/complex setae. Cheliped basis about twice as long as wide; fixed finger with three inner and two ventral simple setae. Pereopod 1 dactylus and unguis combined longest, about 1.6 times as long as propodus and about 28% of pereopod 1 total length. Pereopod 3 with one ventrodistal spiniform seta on merus, carpus and propodus or spiniform seta absent. Pereopods 4 and 5 basis 1.5 to 2.5 times as long as wide; propodus dorsodistal simple seta either marginally longer than- or about twice as long as dactylus and unguis combined. Uropod exopod with one or two articles; endopod with five articles.

Generic remarks. The genus *Intermedichelia* was monotypic, herein we expand with other characters found on *I. jesseri* n. sp.

Intermedichelia jesseri **n. sp.**

(Figures 18–20)

Material examined. Holotype: ovigerous female (REG# MOUFPE 14.323), 3.7 mm body length. Station NE IV #131 (02°23’S 039°89’W). Type locality: Ceará State [CE], Brazil. Depth: 40 m, 20 November 2000.

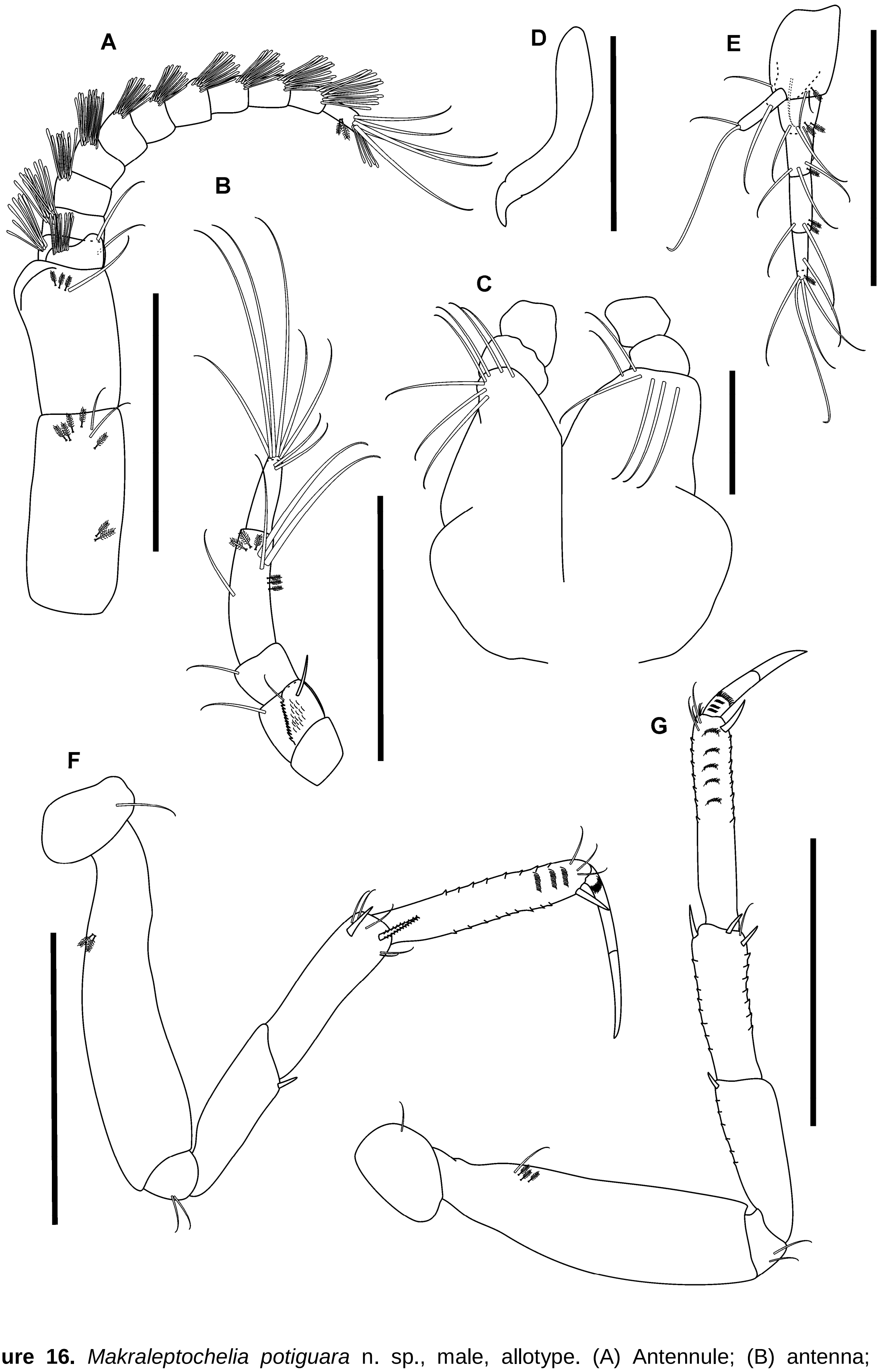


Figure 16. *Makraleptochelia potiguara* n. sp., male, allotype. (A) Antennule; (B) antenna; (C) maxilliped; (D) epignath; (E) uropod; (F) pereopod 1; (G) pereopod 2. Scale bars (A–B; E–G) = 0.5 mm and (C–D) = 0.1 mm.

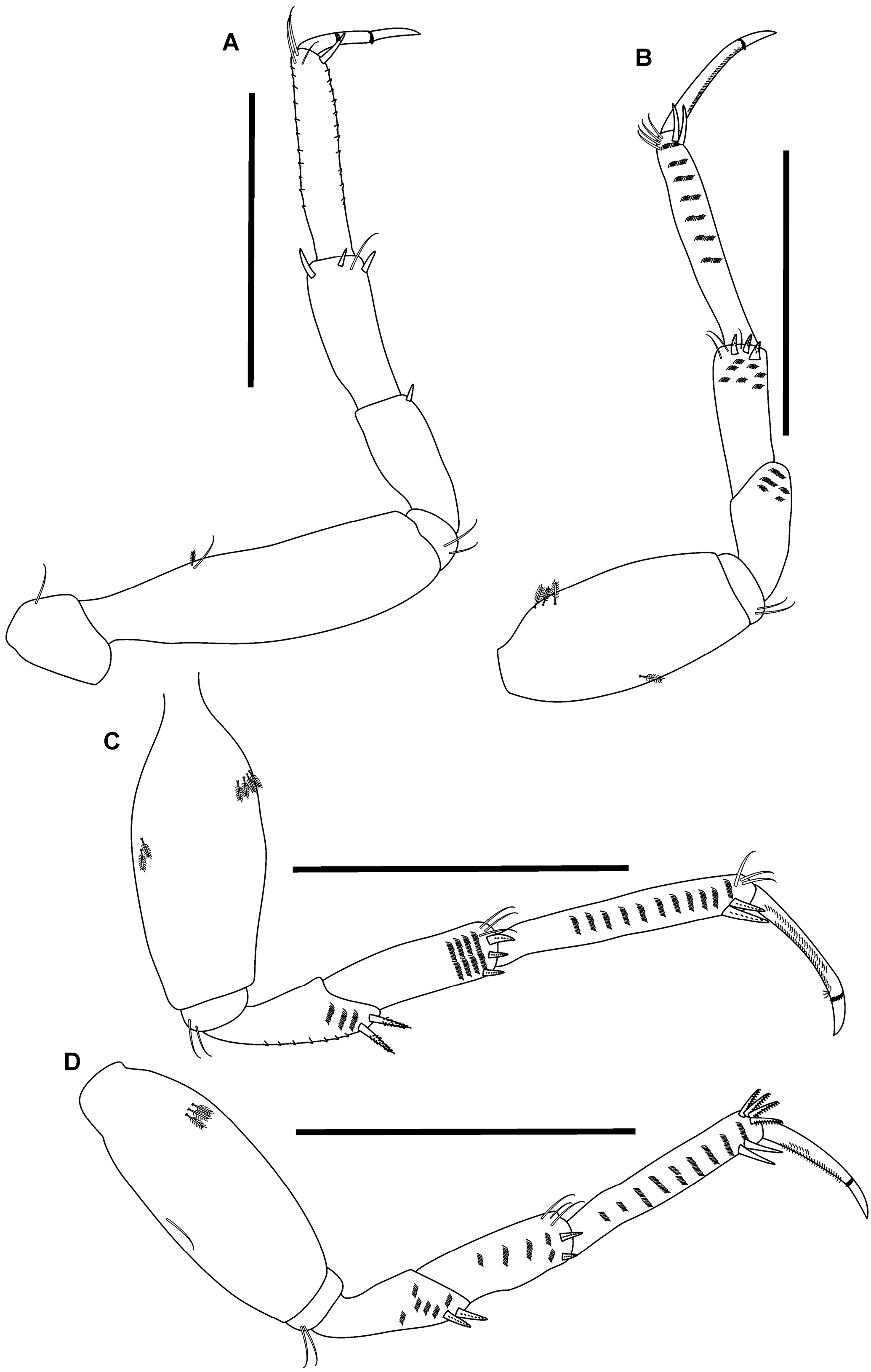


Figure 17. *Makraleptochelia potiguara* n. sp., male, allotype. (A) Pereopod 3; (B) pereopod 4; (C) pereopod 5; (D) pereopod 6. Scale bars (A–D) = 0.5 mm

Paratypes: one female with oostegites (dissected) (REG# MOUFPE 15.069); three females without oostegites (REG# MOUFPE 14.324), same locality of holotype. One female without oostegites (REG# MOUFPE 14.325); station NE IV #178 (011°27'S 037°02'W), 3 December 2000. Specimens were collected in sandy sediment, sorted from algae and sponges, depth: 71.6 m. Locality: Sergipe State [SE], Brazil.

Diagnosis. Female. Lateral projections on pereonite 3 with two distal simple setae. Antennule with several setulated setae. Maxilliped basis with two distal simple setae. Pereopod 3 with one ventrodistal spiniform seta on merus, carpus and propodus. Pereopods 4–6 basis very stout, about 1.5 times as long as wide; propodus dorsodistal seta only marginally longer than dactylus. Uropod exopod uniarticulate.

Etymology. The species is named after of the amphipod specialist and friend Prof. Jesser Fidelis de Souza Filho. The name 'jesseri' is a Latinization of his given name.

Description. Based on holotype (3.7 mm) and paratype, ovigerous female.

Body (Figure 18A): dorsoventrally flattened, about 7.3 times as long as wide. Cephalothorax: about 1.3 times as long as wide, naked, as long as two first pereonites combined. Rostrum short, but visible rounded on top. Triangular eye-lobes and visual elements present. Pereon: about 4.6 times as long as wide, about 64% of total body length and 3.6 times as long as cephalothorax. Pereonite 1 shortest, about two times as long as wide. Pereonites 2, 5 and 6 subequal; with one mediolateral simple seta on each margin. Pereonite 3 with medial lateral projections with two distal simple setae. Pereonite 4 longest, slightly longer than wide. Pleon: about 1.5 times as long as wide and about 25% of total body length. Pleonites subequal, with one or two simple seta on each lateral margin. Pleotelson about twice as long as wide, with one pair of simple setae on medial and posterodistal margins.

Antennule (Figure 20D): of four articles (terminal article reduced), about 1.2 times as long as cephalothorax. Article 1 elongate, 1.5 times as long as following articles combined and 3.7 times as long as wide, with five ventromedial setulated setae, ventrodistal margin with one simple and three setulated setae, one dorsodistal simple seta. Article 2 as long as article 3, with one ventrodistal simple seta, dorsodistal margin with one setulated and one simple seta. Article 3 with five distal simple setae. Terminal article with three simple setae and two aesthetascs.

Antenna (Figure 20E): of six articles (terminal article reduced), about 0.6 times as long as antennule. Article 1 naked. Article 2 as long as article 3, ventral margin with a row of fine simple setules, two simple setae and one strong simple seta distally, one dorsodistal spiniform seta. Article 3 with a row of fine simple setules and one distal simple seta. Article 4 as long as previous articles combined, inner margin with one medial simple seta, one setulated and two distal simple setae, outer margin with one medial simple seta, one setulated, one simple seta and three setulated setae. Article 5 about 0.5 times as long as article 4, with two distal simple setae and one setulated seta. Terminal article with four simple setae.

Mouthparts (Figure 18C–G): Labrum not recovered. Mandibles (Figure 18C, D) molar process broad, with serrate edges (not illustrated). Left mandible (Figure 18C) incisor and lacinia mobilis with six denticles and proximal denticle crenulate. Right mandible (Figure 18D) with about seven denticles. Labium (Figure 18E) with two pairs of lobes, rounded on top, with several fine simple setules on distal margin. Maxillule (Figure 18F) palp uniarticulate, endite with ten distal spiniform setae, with several fine simple setules on each lateral margin. Maxilla not recovered. Maxilliped (Figure 18G) endite with fine simple setules, two complex setae and one simple seta on distal margin; basis about 2.2 times as long as wide, with two distal simple setae. Palp article 1 naked; article 2 with one outer distal simple seta, inner margin with a row of fine simple setules and five simple setae; article 3 as long as article 4, with seven simple setae on inner margin; article 4 with several fine simple setules and eight simple setae. Epignath not recovered.

Cheliped (Figure 20C): attached via sclerite. Basis about 1.9 times as long as wide, with one dorsodistal simple seta. Merus with two ventral simple setae. Carpus about twice as long as wide and slightly longer than basis, dorsal margin with one medial and one distal simple seta, two ventrodistal simple setae. Propodus about 1.2 times as long as wide, inner distal margin with one distal simple seta, four bipinnate setae and two simple setae, outer margin with one short distal simple seta and one long simple next to dactylus insertion. Fixed finger with two ventral simple setae and three simple setae on inner margin. Dactylus and unguis naked, as long as fixed finger.

Pereopod 1 (Figure 19A): coxa with one simple seta. Basis about 3.8 times as long as wide, dorsoproximal margin with one short spiniform seta, one simple seta and two setulated setae. Ischium with two ventral simple setae. Merus about 1.3 times as long as wide, naked. Carpus slightly longer than merus, with two dorsodistal simple setae, ventrodistal margin with three simple setae and one setulated seta. Propodus about 3.7 times as long as wide and 1.4 times as long as carpus, with three subdistal simple setae, ventral margin with two simple setae and one setulated seta. Dactylus and unguis combined about 27% of pereopod 1 total length, about 1.6 times as long as propodus and slightly longer that basis. Unguis slightly longer than dactylus.

Pereopod 2 (Figure 19B): as pereopod 1 except basis dorsoproximal margin with one simple and one setulated seta. Ischium with one ventral simple seta. Merus with one ventrodistal simple seta. Carpus with one dorsodistal simple seta and three ventrodistal simple setae. Propodus about 2.8 times as long as wide, with two dorsodistal simple setae and three ventrodistal simple setae. Dactylus and unguis combined about 0.5 times as long as propodus, with one dorsodistal simple seta. Unguis as long as dactylus.

Pereopod 3 (Figure 19C): as pereopod 2 except merus with one ventrodistal spiniform seta. Carpus with two simple setae and one spiniform seta on ventrodistal margin, one dorsodistal simple seta. Propodus dorsal margin with one medial simple seta, one long and one short spiniform seta distally, one subdistal simple seta.

Pereopod 4 (Figure 19D): no visible coxa. Basis stout, naked, about 1.5 times as long as wide. Ischium with two ventral simple setae. Merus slightly longer than carpus, ventrodistal margin with fine simple setules and one spiniform seta. Carpus with one inner dorsodistal spiniform seta, two outer ventrodistal spiniform setae with medial ring of spinules. Propodus about 2.7 times as long as wide, dorsodistal margin with one setulated seta, two spiniform setae, one circumplumose spiniform seta and one marginally longer than dacytlus and unguis combined, one ventrodistal spiniform seta. Dactylus and unguis combined 0.5 times as long as propodus. Unguis 0.7 times as long dactylus, incompletely fused with dactylus.

Pereopod 5 (Figure 20A): as pereopod 4 except merus each distal margin with one short spiniform seta and one spiniform seta with medial ring of spinules.

Carpus each distal margin with one spiniform seta with medial ring of spinules. Propodus dorsodistal margin with three simple setae (one marginally longer than dactylus and unguis combined), one spiniform and one circumplumose spiniform seta, ventrodistal margin with one simple seta and two spiniform setae.

Pereopod 6 (Figure 20B): as pereopod 5 except basis with one ventromedial simple seta. Merus with two ventrodistal spiniform setae with medial ring of spinules. Carpus with one dorsodistal simple seta. Propodus dorsodistal margin with two simple setae (one as long as dactylus and unguis combined), four spiniform setae and one bipinnate seta, one ventrodistal spiniform seta.

Pleopods (Figure 18B): basal article trapezoidal, with one plumose seta. Exopod with 16 plumose setae and one proximal plumose seta. Endopod with one outer medial plumose seta and 13 inner plumose setae, distal seta with serrate apex.

Uropod (Figure 20F): basal article naked. Exopod uniarticulate, about 0.7 times as long as article 1 of endopod, with two distal simple setae. Endopod of five articles; articles 1, 2 and 4 subequal; article 3 with two simple setae and one setulated seta; article 5 with five distal simple setae.

Geographical distribution. The species of the genus are endemic to the Brazilian coast. Western Mid-Atlantic: Ceará [CE] to Sergipe State [SE], Brazil.

Remarks. *Intermedichelia jesseri* is very similar in body-shape and mouthparts morphology to *I. gracilis*. However, they can be separated by the following combination of characters: 1) the lateral projections of pereonite 3 with two distal simple setae (one in *I. gracilis*), 2) the article 1 of antennule with several setulated setae (absent in *I. gracilis*), 3) the maxilliped basis with two distal simple setae (three in *I. gracilis*), 4) the pereopod 3 with one ventrodistal spiniform seta on merus, carpus and propodus (absent in *I. gracilis*), 5) the pereopods 4–6 with basis much wider (about 1.5 times as long as wide) than in *I. gracilis* (about 2.5 times as long as wide), 6) the pereopods 4–6 propodus

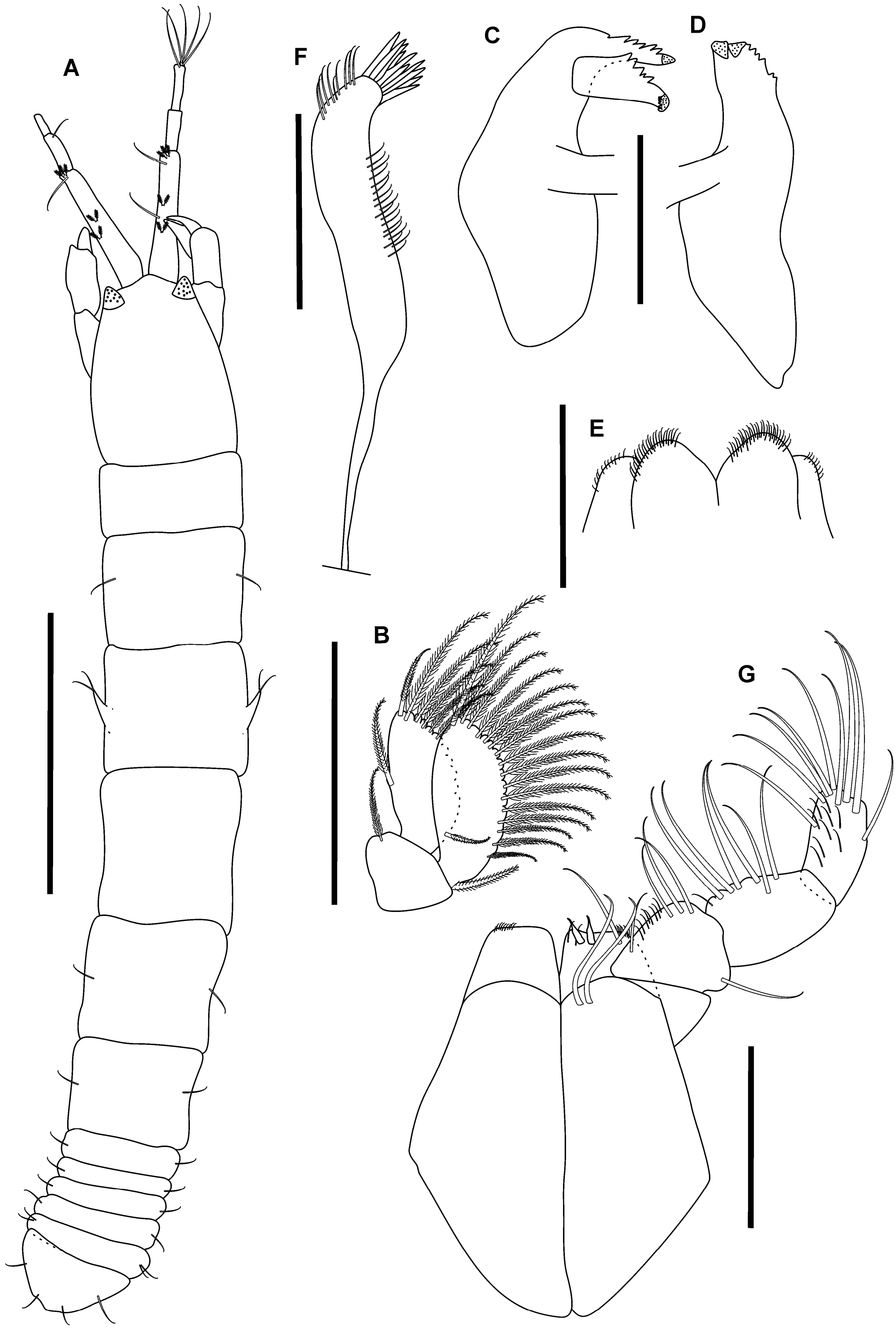


Figure 18. *Intermedichelia jesseri* n. sp., female, holotype. (A) Dorsal view. Paratype, female: (B) pleopod; (C) left mandible; (D) right mandible; (E) labium; (F) maxillule; (G) maxilliped. (A) Scale bar = 1 mm; (B) scale bar = 0.2 mm and (C–G) scale bar = 0.1 mm.

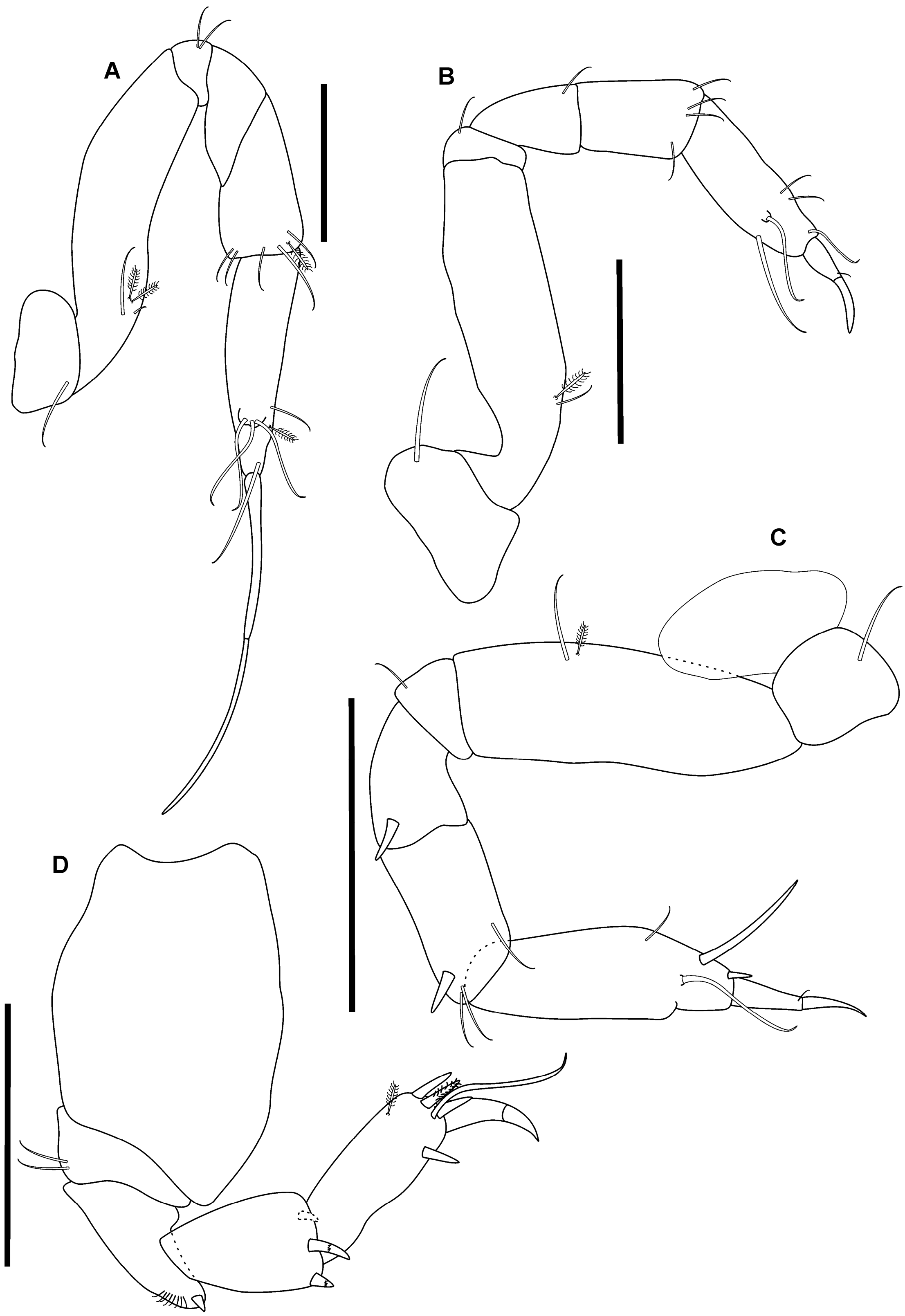


Figure 19. *Intermedichelia jesseri* n. sp., female, paratype. (A) Pereopod 1; (B) pereopod 2; (C) pereopod 3; (D) pereopod 4. (A–D) Scale bars = 0.2 mm.

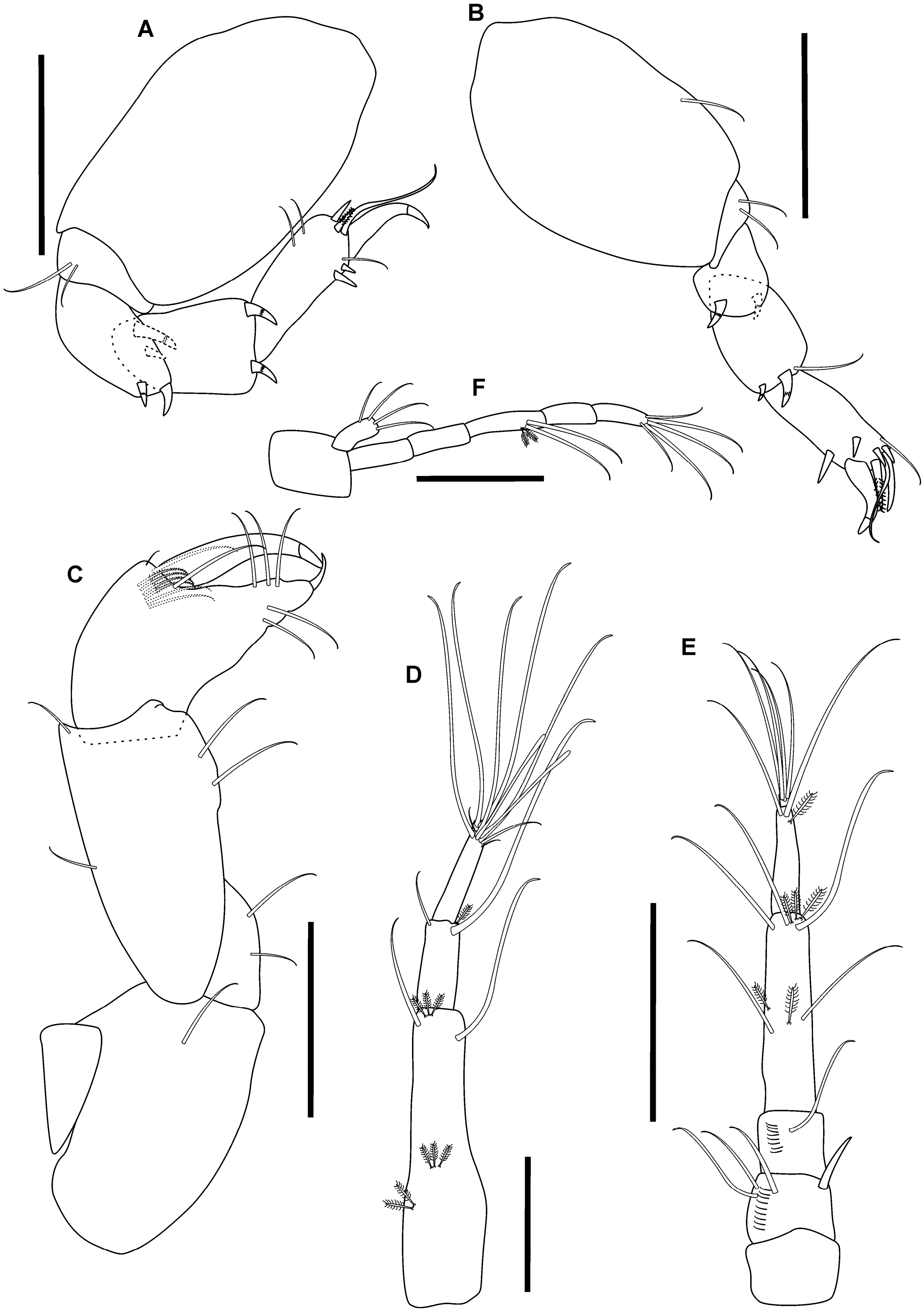


Figure 20. *Intermedichelia jesseri* n. sp., female, paratype. (A) Pereopod 5; (B) pereopod 6; (C) cheliped; (D) antennule; (E) antenna; (F) uropod. (A–E) Scale bars = 0.2 mm and (F) scale bar = 0.1 mm.

dorsodistal seta only marginally longer than dactylus and unguis combined (more than twice as long as dactylus and unguis combined in *I. gracilis*), 7) the uropod exopod uniarticulate (biarticulate in *I. gracilis*). Also Guţu (1996: 113, fig. 37C) illustrates- but do not mention- a strange maxilliped palp configuration where both articles 1 and 2 are attached to the basis. However, we consider this feature an artefact. During the same collection program, we found specimens of *I. gracilis* which confirm the differences between these two species. The only character used by Bird & Larsen (2009: 148 [94]) to remove *Intermedichelia* from the Leptocheliidae was that the propodus of pereopods 4–5 carried modified dorsodistal setae. Since this feature is now shown to vary within the genus, we here transfer *Intermedichelia* to the family Leptocheliidae.

Acknowledgements

The authors would like to thanks PETROBRÁS (Petróleo Brasileiro S/A) and Prof. Paulo Jorge Parreira dos Santos (Universidade Federal de Pernambuco/UFPE) for the concession of part of the data and material; we also give thanks to Dr. Richard Heard and one anonymous reviewer for their criticism. This paper is part of a Ph.D. dissertation (CLAS) funded by CAPES–Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Grant number: 5428/10-6).

References

Araújo-Silva, C.L. & Larsen, K. (2012). Tanaidacea from Brazil. III. New records and description of a species collected from REVIZEE-NE Program. *Nauplius*, 20 (2): 87–105.

Bamber, R.N. (2006). Shallow water tanaidaceans (Crustacea: Peracarida: Tanaidacea) from New Caledonia and the Loyalty Islands. *Zootaxa*, 1108: 1–21.

Bird, G.J. (2011). Paratanaoidean tanaidaceans (Crustacea: Peracarida) from littoral and shallow sublittoral habitats in New Zealand, with descriptions of three new genera and seven new species. *Zootaxa*, 2891: 1–62.

Bird, G.J & Larsen, K. (2009). Tanaidacean Phylogeny: The second step. The basal Paratanaoidean families. *Arthropod Systematics and Phylogeny*, 67: 137–158.

Dana, J.D. (1849). Conspectus Crustaceorum. Conspectus of the Crustacea of the Exploring Expedition. *American Journal of Science and Arts, Series 2*, 8: 424–428.

Edgar, G.J. (2012). New Leptocheliidae (Crustacea: Tanaidacea: Tanaidomorpha) from Australian seagrass and macro-algal habitats, and a redescription of the poorly-known *Leptochelia ignota* from Sydney Harbour. *Zootaxa*, 3276: 1–37.

Guţu, M. (1996). Tanaidaceans (Crustacea, Peracarida) from Brazil, with descriptions of new taxa and systematical remarks on some families. *Travaux du Muséum National d´Histoire Naturelle 'Grigore Antipa'*, 35: 23–133.

Guţu, M. (1998). Malacostraca–Peracarida. Tanaidacea. *In:* Young, P.S. (ed.), Catalogue of Crustacea of Brazil. Rio de Janeiro, Museu Nacional, pp. 549–557.

Guţu, M. (2011a). The redescription of the species *Leptochelia bispinosa* Guţu and *L. corsica* Dollfus, and the first description of the female of *L. tenuicula* Makkaveeva (Crustacea: Tanaidacea). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'*, 54: 21–41.

Guţu, M. (2011b). A new genus and two new species of leptocheliids from the marine shallow waters of Indonesia (Crustacea: Tanaidacea: Tanaidomorpha). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa*', 54: 43–61.

Krøyer, H. (1842). Nye Arter af Slægten Tanais. *Naturhistorisk Tidskrift*, 4:167–188.

Lang, K. (1973). Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen (Crustacea). 8. Die Gattungen *Leptochelia* Dana, *Paratanais* Dana, *Heterotanais* G.O. Sars und *Nototanais* Richardson. Dazu eininge Bemerkungen über die Monokonophora und ein Nachtrag. *Zoologica Scripta*, 2: 197–229.

Larsen, K. (2003). Proposed new standardized anatomical terminology for the Tanaidacea (Peracarida). *Journal of Crustacean Biology*, 23: 644–661.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny, the first step: the superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research*, 40, 205–222.

Larsen, K., Araújo-Silva, C.L. & Coelho, P.A. (2009). Tanaidacea from Brazil. I. The family Tanaellidae Larsen & Wilson, 2002. *Zootaxa*, 2141: 1–19.

Masunari, S. (1983). Postmarsupial development and population dynamics of *Leptochelia savignyi* (Krøyer, 1842) (Tanaidacea). *Crustaceana*, 44: 151–162.

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzieger*, 205: 401–416.

Silva-Brum, I.N. (1973). Contribuição ao conhecimento da fauna do Arquipélago de Abrolhos, Bahia, Brasil, Nº 4. Crustacea–Tanaidacea. *Boletim do Museu de História Natural da Universidade Federal de Minas Gerais, Zoologia*, 18: 1–14.

Stebbing, T.R.R. (1896). A new West-Indian tanaid. *Annals and Magazine of Natural History, Series 6*, 17: 49–53.

urn:lsid:zoobank.org:pub:F53ADCA2-1415-4357-ABC0-04D82C730466

Crustaceana, 86 (2): 221–245 (2013)

Article 3. Tanaidacea (Peracarida) from Brazil. V. Two new species of *Apseudes* Leach, 1814 from the Northeastern coast of Brazil

Catarina L. Araújo-Silva [1,3], Petrônio A. Coelho[2]† & Kim Larsen[1]

1) Laboratory for Marine Community Ecology and Evolution, CIIMAR (Centro Interdisciplinar de Investigação Marinha e Ambiental), University of Porto, Rua dos Bragas 289, P-4050-123 Porto, Portugal. 2) Laboratory of Carcinology, Museum of Oceanography 'Petrônio Alves Coelho', Departament of Oceanography, Federal University of Pernambuco, Av. Arquitetura S/N, 50740-550 Recife, Pernambuco, Brazil. 3) Capes Foundation, Ministry of Education of Brazil, Brasília-DF 70040-020, Brazil. Correspondig author: e-mail: katelas@hotmail.com

Abstract

Collections made during the REVIZEE program along the continental shelf, oceanic banks of the Archipelago of Fernando de Noronha and the North Chain Banks of Brazil, revealed a number of tanaidaceans species belonging to the genus *Apseudes* (Apseudidae). Two new species, *Apseudes noronhensis* and *A. aisoe*, are described here as is the first record of the genus *Apseudes* in Brazilian waters. Several diagnostic characters attributed to *Muramurina* were found during this study to be inconsistent and *Muramurina* is here suggested as being a junior synonym of *Apseudes*.

Resumo

Coletas realizadas durante o Programa REVIZEE ao longo da plataforma continental, bancos oceânicos do Arquipélago de Fernando de Noronha e os Bancos da Cadeia Norte do Brasil, revelaram exemplares de tanaidáceos pertencentes ao gênero *Apseudes* (Apseudidae). São descritas duas novas espécies, *Apseudes noronhensis* e *A. aisoe*, e o primeiro registro do gênero *Apseudes* em águas brasileiras. Diversos caracteres diagnósticos atribuídos ao gênero *Muramurina* foram encontrados nos espécimes estudados e considerados

inconsistentes, portanto, *Muramurina* é aqui sugerido como sendo sinônimo júnior de *Apseudes*.

Introduction

This is the fifth paper on the systematics of the Tanaidacea from Brazil based on collection programmes made by the Brazilian government. It is also the third in a series of papers on northeastern Brazil.

During the REVIZEE Program (for details, see Araújo-Silva & Larsen 2012) collections were made along the continental shelf and oceanic banks of the Archipelago of Fernando de Noronha and North Chain Banks of Brazil. These collections revealed a number of members of the family Apseudidae Leach, 1814 belonging to the genus *Apseudes* Leach, 1814, and are the focus of this study.

The family Apseudidae has a global distribution, and is the largest tanaid family, with almost 170 described species (Anderson 2012). There is general consensus that the Apseudidae are too crowded and the diagnosis of the family has changed several times in recent years (Guţu 2002, 2006, 2007a, 2008; Błazewicz-Paszkowycz & Larsen 2004; Araújo-Silva & Larsen 2010; Larsen *et al*. 2011).

The diagnosis of the type species, *Apseudes talpa* (Montagu, 1808) and, thus, also the diagnosis of the type genus, *Apseudes*, was changed by Larsen *et al*. (2011), due to the presence of simultaneous hermaphroditism (i.e. specimens with both a penal cone and oostegites), while some had either male or female cheliped morphology.

The ‘female’ cheliped was defined as lacking a process on the fixed finger and a longer ventral carpus margin relative to the length of the propodus; while the ‘male’ cheliped was defined as having a process on the fixed finger and shorter ventral carpus margin relative to the length of the propodus. These findings were supported by genetic evidence that confirmed the presence of only one species despite the difference in cheliped morphology expressions. Larsen *et al.* (2011) thus synonymized the genus *Androgynella* Guţu, 2006 with *Apseudes*, but not *Muramurina* Guţu, 2007b, which was not examined in that study.

The species described in this study were first thought to belong to the genera *Androgynella* and *Muramurina*. However, when compared with other species of the genus, we found a number of inconsistencies in the generic diagnoses (see Table 2). Here we consider *Muramurina* as a junior synonym of *Apseudes* (see systematics remarks section). *Muramurina* was first erected as *Muramura* by Guţu (2006) but the name was changed by Guţu (2007b) since the name was preoccupied by a genus of *Marsupialia*.

Material and Methods

Specimens were collected from the continental shelf between the Foz do Rio Parnaíba (Piauí State (PI)) and Salvador (Bahia State (BA)), from the Archipelago of Fernando de Noronha, and from the North Chain Banks of Brazil (see Figure 21). The expeditions Northeast I (NE I) (1995), III (NE III) (1998) and IV (NE IV) (2000) were funded by the Brazilian Government and conducted from the RV 'Antares' (Directorate of Hydrography and Navigation). The material was collected by a rectangular dredge with a mesh size of 0.5 mm and a capacity of about 70 L of sediment, with lateral expansions that allowed dredging only in the first 10 cm of the surface sediment for five minutes in accord to the methodology proposed by Holme & McIntyre (1984).

Body length was measured from the anterior margin of the carapace rostrum to the tip of the telson in lateral view to avoid bias from a flexed body posture. Body width was measured on the widest part of the carapace in dorsal view. Terminology follows Larsen (2003). Dissections were made with chemically sharpened tungsten wire needles and then placed on slides with glycerin, covered by a cover slip and sealed with nail polish. Whole animal illustrations were made from holotype specimens while appendages were dissected and drawn from paratypes via a camera lucida attached to a Leica compound microscope. Drawings were made with the aid of the computer program CorelDraw. Type material is kept at the Carcinological Collection of the Museu de Oceanografia 'Petrônio Alves Coelho' da Universidade Federal de Pernambuco (MOUFPE).

Lang (1953: 410–411), already rejected the use of hyposphenians as a useful character since these are quite variably within a species and indeed disappear entirely during brooding. We have therefore illustrated these but do not consider them diagnostic.

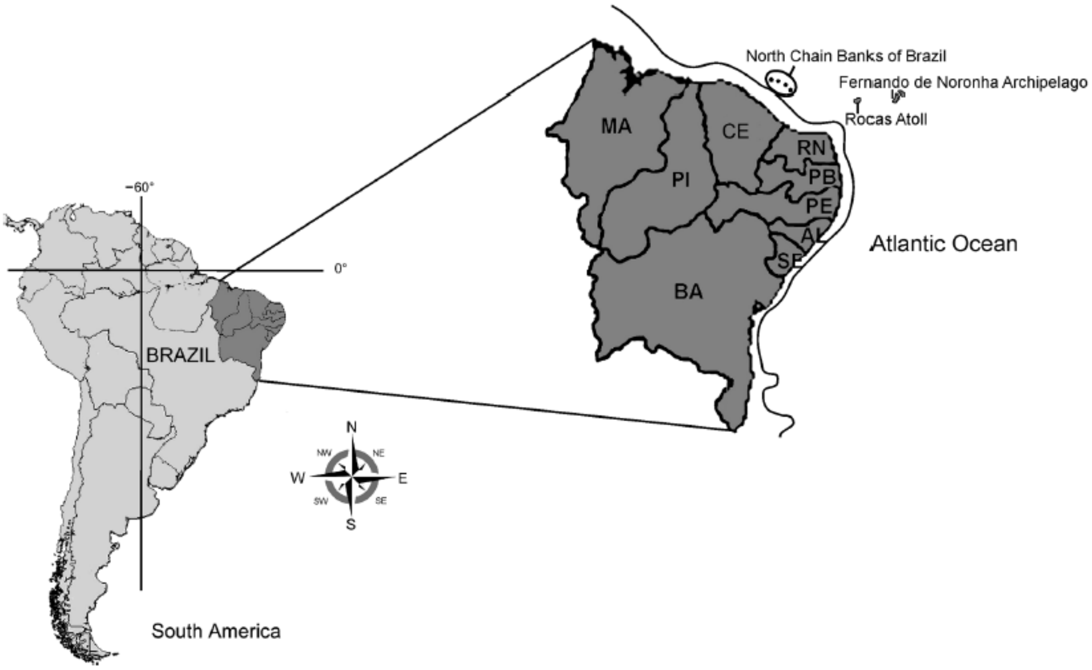


Figure 21. Map of the study area, northeastern coast of Brazil, indicating the continental shelf, North Chain Banks of Brazil and Fernando de Noronha Archipelago.

Table 2. List of diagnostic characters based on Guţu (2006, 2007a) with additional characters to separate the new species of *Apseudes* and closely related species. Abbreviations: mxlp, maxilliped; RM, right mandible; LM, left mandible; MB, mandible; A1, antennule; A2, antenna; Ptl, pleotelson; spin., spiniform; art, article.

Taxa	**Total body length**	**Carapace length 1^{st} art.of A1**	**Type of seta of carapace**	**Ptl. prop.**	**Ptl. longer than any pereonite**	**Type of seta on inner margin of 1^{st} art. of A1**	**Type of seta on A2 squama**	**Relative length of 2^{nd} and 1^{st} art of MB palp**	**Relative length of 2^{nd} and 3^{rd} MB palp**	**N° spin. seta on outer distal margin 2^{nd} art mxlp.**	**Type seta on inner margin of 2^{nd} art. of mxlp. palp**	**Dorsodistal spine on cheliped carpus**	**Type of seta on P6**
Apseudes aisoe **n. sp**.	4-5 mm	1.4×	Simple	1.2×	Longer	Simple	Simple	4×(RM) 2.2× (LM)	≈ 1.8× (RM) 1.8× (LM)	2	Simple	Absent	Plumose
A.crozetensis Shiino,1978	14.5 mm	1.7×	Absent	1.7×	Longer	Plumose	Plumose	2.3×	2.1×	1	Simple	Present	Plumose
A. curtiramus (Guţu,2007a)	4-6 mm	2.4×	Plumose	1.3×	Longer	Plumose	Simple	2.5× (2.2×)***	2×	1	Simple	Absent	Plumose
A.fecunda (Guţu, 2006)	15 mm	2×	Plumose	1.8×	Longer	Plumose	Plumose	2.1×	1.7×	3	Plumose	Absent	Plumose
A. nagae Shiino, 1963	9.1 mm	≈ 1.4×	Plumose	1.7×	Longer	Plumose	Plumose	1.7×	2.1×	2	Plumose	Absent	Plumose
A. nhatrangensis Shiino, 1963	9-10 mm	2×	Plumose	2×	Longer	Plumose	Plumose	1.7×	≈ 1.5x	3 or 4	Plumose	Absent	Plumose
A.nipponicus Shiino, 1937	16 mm	1.6×	Simple	2.3×	Longer	Not recorded	Simple	1.8×	1×	3	Simple	Present	Plumose
A. noronhensis **n. sp.**	8-9 mm	2×	Simple	1.3×	Longer	Plumose	Simple	2.8× (RM) 3.3× (LM)	1.6× (RM) 1.6× (LM)	2	Plumose	Present	Plumose
A.spectabilis (Studer,1884)**	3.2 mm	1.8×	Absent	1.3×	Longer	Plumose	Plumose	3.5×	2×*	1	Simple	Not recorded	Plumose
A.(=Muramurina)fagettii Báez & Magnere, 1980	3.3 mm	2×	Simple	1.8×	Longer	Simple	Simple	2×	1.3×	1	Simple	Absent	Plumose
A. (= Muramurina) splendida (Guţu, 2006)	3.8 mm	1.3×	Simple	1.2×*	Shorter*	Plumose	Simple	≈ 2.8×	1.1×	1	Simple	Absent	Plumose

* Measurement not realistic, since most of the dorsal view drawings do not show the curvature of some appendages in tanaids.

** Based on Lang (1953) and Larsen & Shimomura (2006).

*** Measured as in Guţu (2007a: 49).

For “seta”, please read “setae” where relevant.

Results

TAXONOMY

Order TANAIDACEA Dana, 1849

Suborder Apseudomorpha Sieg, 1980

Family Apseudidae Leach, 1814

Genus *Apseudes* Leach, 1814

Apseudes noronhensis **n. sp**.

(Figures 22–25)

Material examined. Holotype: simultaneous hermaphrodite with oostegites (Reg. Nº MOUFPE 14.282), 9 mm. Station NE III #93, 2 June 1998, coordinates: 03°75S 32°33W. Fernando de Noronha Island, Pernambuco State (PE), Brazil; water depth: 70 m.

Paratype: one simultaneous hermaphrodite with oostegites (dissected) (Reg. Nº MOUFPE 14.283), 8.4 mm. Same locality as the holotype. All specimens were collected in gravel sediment and algae.

Diagnosis: simultaneous hermaphrodite with oostegites. Carapace with six simple setae in ocular region. Pereonites 1–3 with rounded expansions on anterolateral margin. Antenna with more than 15 articles; article 2 ventral margin with three proximal spines and two distal spines; article 3 with one spiniform seta on ventrodistal margin. Mandible palp article 2 about three times as long as article 1. Maxilliped basis with one spiniform seta and two serrated setae on inner margin. Cheliped carpus with one dorsodistal spine. Uropod with more than 40 serially repeating articles on endopod and nine on exopod.

Description. Body from holotype, appendages from dissected paratype.

Body (Figure 22A, B): heavily calcified. Dorsoventrally flattened. Long, about 6.3 times as long as wide. With numerous plumose setae on dorsal and lateral view. Cephalothorax: as long as wide, about 20% of total body length with grooves in the anterior and posterior portions of dorsal margin. Rostrum with sharp notches at base, tip pointed. With long ventral hyposphenians. With one depression on posterior region next to eye lobes. Ocular lobes present but visual elements absent, with six lateral simple setae. Pereon (Figure 22B): about 52% of total body length and 2.7 times as long as wide, with plumose setae throughout dorsal and lateral margins. Pereonite 1 slightly wider and shorter than other pereonites. Pereonites 2–5 with short ventral hyposphenians. Pereonites 2–4 with rounded anterolateral projections and several plumose setae; posterior margin with two plumose setae. Pereonites 5 and 6 subequal, anterolateral margin with pointed projection. Pereonite 6 with ventral penal genital cone (Figure 22B). Pleon: about 28% of total body length; about 1.7 times as long as wide. Pleonites short, five times as wide as long; with several plumose setae on both lateral margins and few along dorsal margin. Pleotelson about 1.3 times as long as wide with several plumose setae on lateral margins.

Antennule (Figure 23A): peduncle article 1 about 0.5 times as long as cephalothorax; three times as long as wide, with eleven plumose setae, four simple and five setulated setae; several proximal short spines on both lateral margins. Peduncle article 2 at least three times as long as article 3 with ten plumose setae and two simple setae. Peduncle article 3 as long as peduncle article 4, with six plumose setae. Peduncle article 4 (common article) with one setulated seta. Outer flagellum (articles counted from holotype, since paratype is broken) with 17 serially repeating articles each with at least one or two simple setae; articles 4, 6 and 8 with aesthetasc. Inner flagellum with seven serially repeating articles; articles with one-three simple setae on each article and six long simple setae on terminal article.

Antenna (Figure 23B): 17 articles, about 0.7 times as long as antennule. Article 1 expanded internally accompanied by five short distal spiniform setae and two simple setae. Article 2 as long as following two articles combined; three spines and one simple seta on inner proximal margin; inner distal margin with two spines and two simple setae; outer medial margin with one simple seta. Squama as long as article 2, with 12 long simple setae. Article 3 short with one spiniform seta and one long simple seta on inner distal margin. Article 4 with one inner proximal simple seta and one distal setulated seta. Article 5 as long as article 4; with one setulated seta on outer medial margin; inner margin with one medial simple seta, two setulated setae and two simple setae distally. Article 15 with one setulated seta. Articles 6–16 serially repeating, with one-five long and short simple setae. Terminal article with four long simple setae.

Mouthparts (Figure 24A–F): labrum not recovered. Mandibles (Figure 24A, B, B1) molar typical for Apseudidae, long, broad with heavily chitinous apex, with tooth-like prolongation. Palp triarticulate about four times as long as wide. Article 1 shorter than other articles, with four or five simple setae. Article 2 about three times as long as article 1 and 1.6 times as long as article 3; with ten-11 simple setae and seven setulated setae. Article 3 about 1.8 times as long article 1; with 13 subequal simple setae, three serrated setae and one long terminal simple seta. Left mandible (Figure 24A) incisor and lacinia mobilis well developed, both with four denticles; setal row with six distal bifurcate setae and one bipinnate seta arising from a common peduncle. Right mandible (Figure 24B) incisor with three denticles; setal row (Figure 24B1) with five bifurcate setae and two simple setae of which the most proximal is rather thin, all arising from a common peduncle. Labium (Figure 24C) palp with several setae and denticles on outer and distal margins, three distal spiniform setae; lobes with several fine simple setae on inner and lateral margins. Maxillule (Figure 24D) palp biarticulate; distal article with one long distal serrated seta and five short serrated setae; outer and inner endites with several fine setae on lateral margins; outer endite with ten terminal spiniform setae and two subdistal bipinnate setae; inner endite with five distal circumplumose setae. Maxilla not recovered. Maxilliped (Figure 24E, E1) basis about 1.5 times as long as wide; inner margin with one spiniform seta and two serrated setae. Endite (Figure 24E1) distal margin with about ten complex and two simple setae; ventral margin with four coupling hooks, one spiniform seta, and about 11 circumplumose setae, inner margin also with a row of simple setae. Palp article 1 shorter than article 2; with one long simple seta on inner distal margin and one spiniform seta on outer margin. Article 2 slightly shorter than basis; with two spiniform setae on outer distal margin which one longer than article 3; with row of 12 short simple setae and several plumose setae. Article 3 longer than wide; with ten simple setae. Article 4 shorter than other articles; with ten simple setae and three terminal pinnate setae. Epignath (Figure 24F) with one stout circumplumose terminal seta.

Cheliped (Figure 23C): exopod triarticulate, with five plumose setae. Basis about 2.5 times as long as wide; with one dorsoproximal seta; one short spiniform seta and three simple setae on ventroproximal margin, one simple and one long spiniform seta on ventromedial margin, three ventrodistal simple setae. Merus with eight simple setae on ventral margin. Carpus slender, about 3.7 times as long as wide; with seven simple setae on ventral margin; with two dorsoproximal simple setae, one spine and one simple seta on dorsodistal margin. Propodus with eight simple setae. Fixed finger with about 11 subequal simple setae and nine denticles on inner margin, seven simple setae on ventral margin. Dactylus with three dorsodistal simple setae.

Pereopod 1 (Figure 25A, A1): not illustrated at same scale to other pereopods. Fossorial type. Coxa with prominent apophysis, seven distal simple setae (not illustrated). Exopod (Figure 25A1) triarticulate with one simple seta on article 1, six plumose setae on article 3. Basis about 2.5 times as long as wide; with two simple setae on dorsoproximal margin; one spine and one simple seta on ventroproximal margin, one spiniform, one simple and one setulated seta on ventrodistal margin. Ischium with three simple setae on ventral margin. Merus longer than wide and each following article; with one long spiniform seta and five simple setae on dorsodistal margin; one spiniform seta and seven simple setae on ventral margin. Carpus as long as propodus and slightly longer than dactylus; with one spiniform seta and 12 simple setae on dorsodistal margin, one spine and two simple setae on outer distal margin; four simple setae and two spiniform setae on ventrodistal margin. Propodus about 1.3 times as long as dactylus and unguis combined; with two spiniform setae and six simple setae on dorsal margin; three spiniform setae and six simple setae on ventral margin. Dactylus with four ventral denticles and two fine simple setae on dorsal margin. Unguis pointed and curved, one-third of total length of dactylus and unguis combined.

Pereopod 2 (Figure 25B): shorter than pereopod 1. Coxa damaged. Basis slender, about 3.5 times as long as wide, at least two times as long as merus; with two dorsoproximal simple setae and 14 simple setae on ventral margin. Ischium with one dorsodistal simple seta and four ventrodistal simple setae. Merus slightly longer than carpus; with one long spiniform seta and four simple setae on dorsodistal margin; three ventroproximal simple setae, three spiniform and two simple setae on ventrodistal margin. Carpus about 0.7 times as long as propodus; ventral margin with two short spiniform setae and one long, two simple setae; ten simple setae and one spiniform seta on dorsodistal

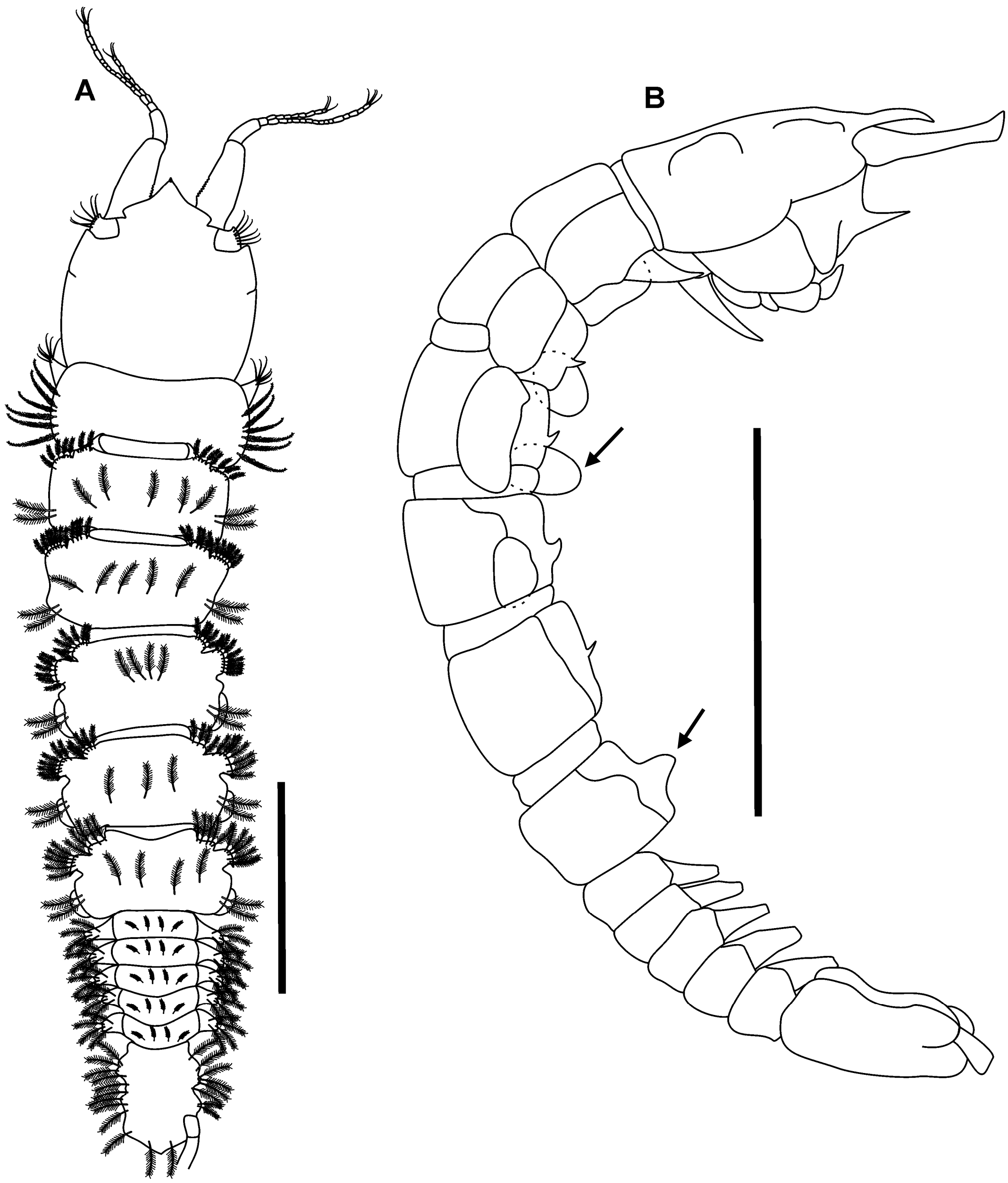


Figure 22. *Apseudes noronhensis* n. sp., simultaneous hermaphrodite. Holotype (Reg. Nº MOUFPE 14.282). (A), Dorsal view; (B), lateral view. Anterior seta: female oostegite on pereonite 3; posterior seta: male genital cone on pereonite 6. Scale bar: 2 mm.

margin. Propodus about 1.7 times as long as dactylus and unguis combined; with three spiniform setae and seven simple setae on dorsal margin; two long and two short spiniform setae, interspersed with five simple setae on ventral margin; one comb seta near insertion of dactylus. Dactylus with two dorsomedial simple setae. Unguis as pereopod 1.

Pereopod 3 (Figure 25C): as pereopod 2 except for: basis with two pairs of plumose setae on dorsal and ventral margins; with seven simple setae on ventral margin. Merus about 0.7 times as long as carpus; with one long simple seta on dorsodistal margin; ventrodistal margin with three simple and three spiniform setae, three ventromedial simple setae. Carpus as long as propodus; with five dorsodistal simple setae; three ventral simple setae. Propodus about 1.2 times as long as dactylus and unguis combined; with one setulated seta and one simple seta on dorsomedial margin, three spiniform setae and three simple setae on dorsodistal margin; two simple setae and one spiniform seta on ventromedial margin. Dactylus with three dorsomedial simple setae and two simple setae on each margin next to insertion of unguis. Unguis pointed and curved, thinner and slightly longer than previous pereopods.

Pereopod 4 (Figure 25D): coxa damaged. Basis three times as long as wide; with six plumose and three setulated setae on dorsal margin; ventral margin with one proximal simple seta, one medial setulated and four distal simple setae. Ischium with five ventral simple setae and one simple on dorsodistal margin. Merus about 0.8 times as long as carpus; with one dorsodistal simple seta; ventral margin with five spiniform setae, two plumose and four simple setae. Carpus about 1.2 times as long as propodus; with seven spiniform and three simple setae on ventral margin. Propodus about 1.5 times as long as dactylus and unguis combined; with one dorsoproximal setulated seta and one simple seta, one dorsomedial simple seta, several pinnate setae on dorsodistal margin which three longer than dactylus; four spiniform setae and four simple on ventral margin. Dactylus shorter than other pereopods; with one pair of simple setae on ventral and dorsal margins; four short denticles on ventral margin. Unguis pointed and curved, about 23% of total length of dactylus and unguis combined.

Pereopod 5 (Figure 25E): as pereopod 4 except for: basis with one proximal setulated seta and ten plumose setae on dorsal margin; ventral margin with one medial simple seta and four distal simple setae. Merus with one spiniform seta and one simple on dorsodistal margin; ventral margin with four medial simple setae, two distal spiniform setae, one distal plumose and one simple seta. Carpus with five dorsal plumose setae; ventral margin with three spiniform and five simple setae. Propodus about 1.2 times as long as dactylus and unguis combined; ventral margin with two spiniform setae, a row of pinnate setae and two simple setae; one simple and one setulated seta on dorsomedial margin, three spiniform setae, one plumose and one simple seta on dorsodistal margin. Dactylus with two denticles on ventral margin and three simple setae on dorsomedial margin. Unguis as in pereopod 3.

Pereopod 6 (Figure 25F): coxa without setae. Basis with ten plumose setae accompanied by five simple setae on dorsal margin; 12 plumose and one fine distal simple setae on ventral margin. Ischium with one pair of plumose and simple setae on ventral margin. Merus as long as carpus; with five plumose setae on dorsal margin; seven plumose setae and one simple seta on ventral margin. Carpus about 1.3 times as long as propodus; with eight plumose setae on dorsal margin; eight plumose setae, one simple and one spiniform seta on ventral margin. Propodus as long as dactylus and unguis combined; with one medial setulated seta, three spiniform and one plumose seta on dorsodistal margin; a row of distal pinnate setae on dorsal and ventral margins (30–35), one spiniform and one simple seta on ventral margin. Dactylus with two denticles, one ventrodistal and two dorsomedial simple setae. Unguis as pereopod 3.

Pleopods (Figure 23D): basal article biarticulate; with six plumose setae on article 2. Endopod with 20 long and plumose setae. Exopod with 16 plumose setae.

Uropods (Figure 23E): long, basal article with three plumose setae. Endopod with 40–45 subequal articles; with one-three simple setae distributed on articles. Exopod with nine articles and simple setae distributed on articles.

Remarks. *Apseudes noronhensis* n. sp. is closely related to *A. orghidani* Guţu & Iliffe, 1989, which was collected from a cave in Bermuda. They share characters as: body proportions; distinct short spines and plumose setae on the inner and outer margins of the antennular peduncle segment 1; the two dorsodistal spiniform setae of article 2 of the maxillipedal palp. However, the new species can be distinguished from *A. orghidani* and other species of the genus due to the following combination of characters: (1) pereonites 1–3 with rounded expansions on anterolateral margin (pointed in *A. orghidani*, except for pereonite 2); (2) antenna with 17 articles (nine in *A. orghidani*); (3) antenna article 2 with three proximal spines and two distal spines on ventral margin (*A. orghidani* with inner margin of article 1 finely denticulate as in article 3); (4) antenna article 3 with one spiniform seta on ventrodistal margin (no spiniform seta on article 3 of *A. orghidani*);

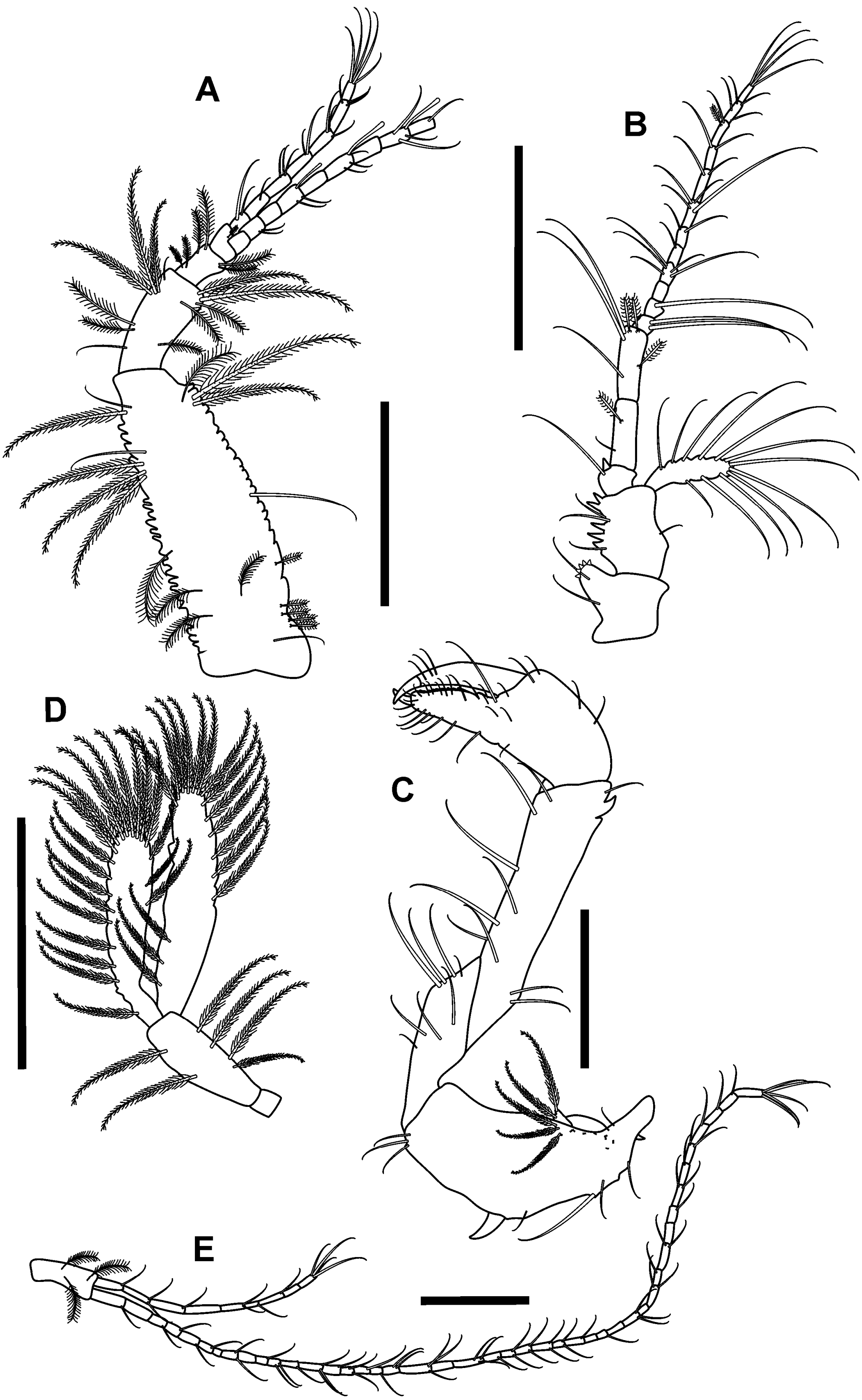


Figure 23. *Apseudes noronhensis* n. sp., simultaneous hermaphrodite. Paratype (Reg. Nº MOUFPE 14.283). (A), Antennule; (B), antenna; (C), cheliped; (D), pleopods; (E), uropods. Scale bars: 0.5 mm.

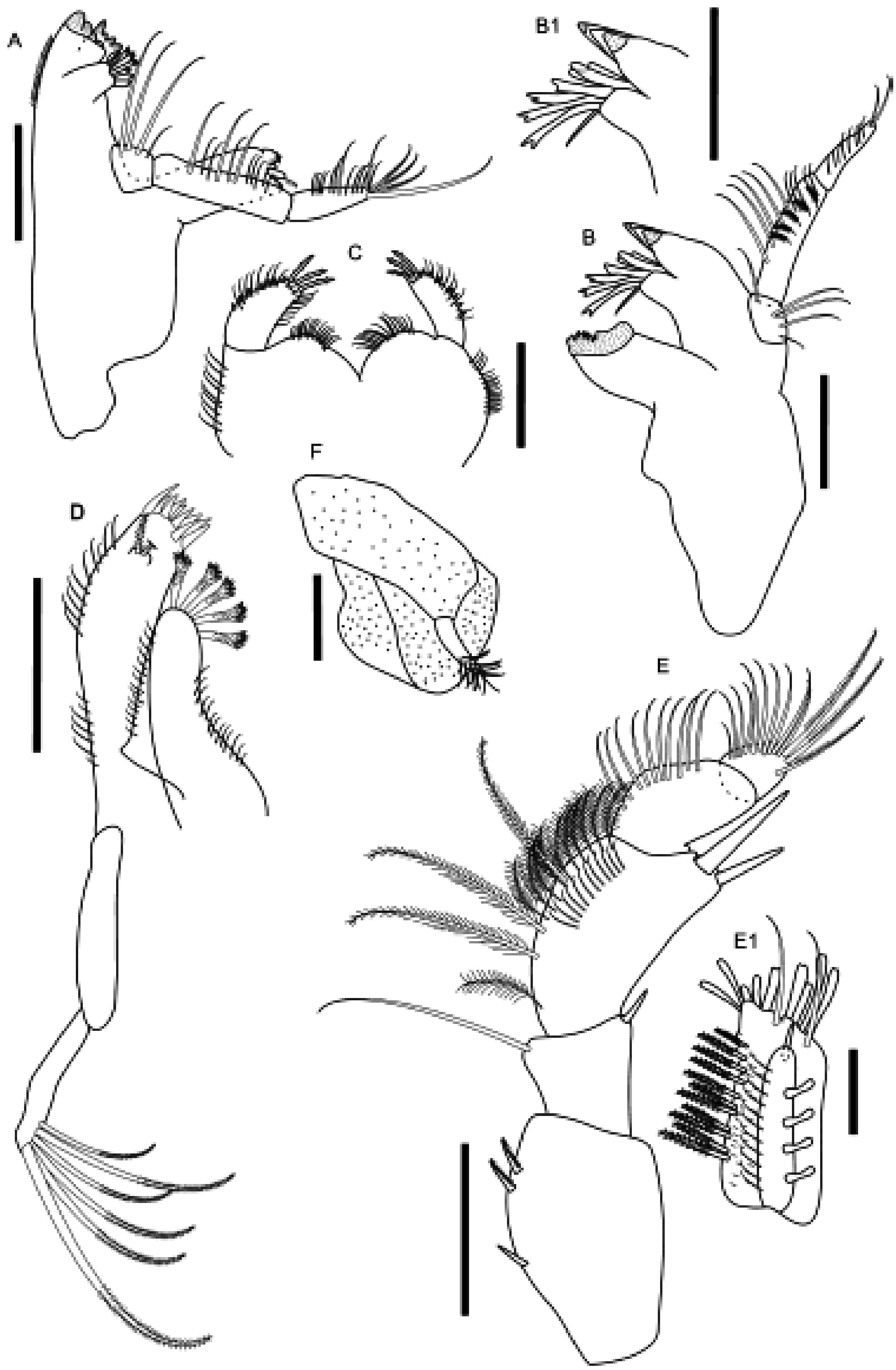


Figure 24. *Apseudes noronhensis* n. sp., simultaneous hermaphrodite. Paratype (Reg. Nº MOUFPE 14.283). (A), Left mandible; (B), right mandible; (B1), detail of right mandible setal row; (C), labium; (D), maxillule; (E), maxilliped; (E1), maxilliped endite; (F), epignath. Scale bars: (A-F), 0.2 mm; (E1), 0.1 mm.

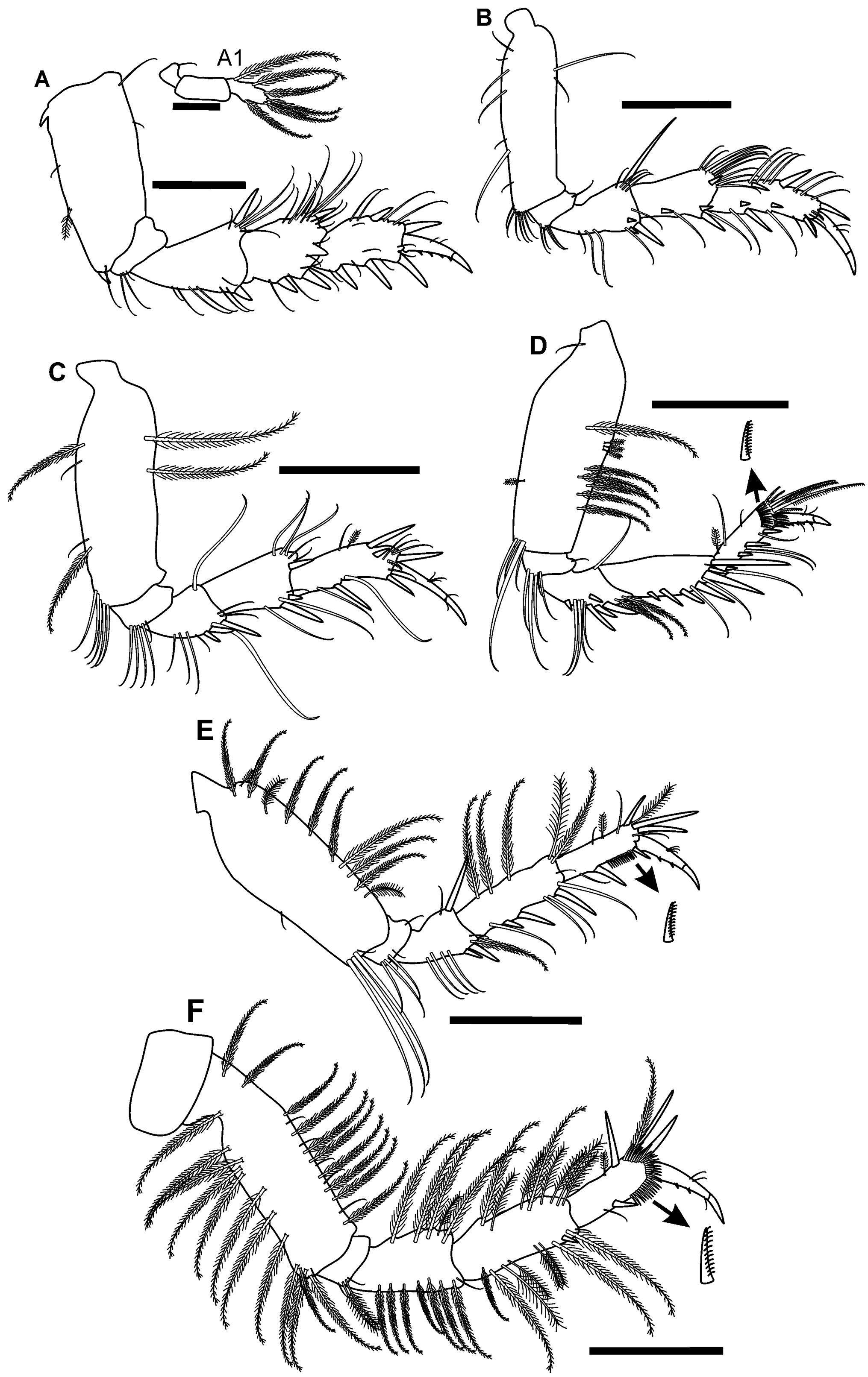


Figure 25. *Apseudes noronhensis* n. sp., simultaneous hermaphrodite. Paratype (Reg. Nº MOUFPE 14.283). (A), Pereopod 1; (A1), exopod; (B), pereopod 2; (C), pereopod 3; (D), pereopod 4; (E), pereopod 5; (F), pereopod 6. Scale bars: (A-F), 0.5 mm; (A1), 0.1 mm.

(5) cheliped carpus with one dorsodistal spine (absent in *A. orghidani*); (6) pereopod 1 with distinct spine on subdistal margin of carpus (absent in *A. orghidani*); (7) pereopod 2 with simple setae on basis (plumose setae in *A. orghidani*). *Apseudes noronhensis* also shares characters with *A. crozetensis* Shiino, 1978 and *A. nipponicus* Shiino, 1937 like the dorsodistal spine on the cheliped carpus and the type of seta on the inner margin of article 1 of the antennule; but they can be easily separated by the lateral spines on the anterior margin of the cephalothorax in *A. crozetensis* (absent in *A. noronhensis*); lateral projection of pereonites 2–6 in *A. crozetensis*; 3–6 in *A. nipponicus* (pereonites 5 and 6 in *A. noronhensis*); spines in antenna article 2 absent in *A. crozetensis* and *A. nipponicus* (versus *A. noronhensis* with three proximal spines and two distal spines on ventral margin).

The type locality of *A. orghidani* is Cripplegate Cave (Bermuda Island) in the North Atlantic and apart from the morphological differences we must also take into consideration the difference in type locality and habitat. The new species was found in warm waters (Fernando de Noronha Island) at depths between 60–70 m and, according to Larsen (2005, 2006), such a wide distribution of a species without planktonic larval stages is unlikely. This also supports the species separation.

Since the genus *Apseudes* contains close to 50 species, many of which are poorly described, it is not possible to make detailed comparisons with all species in this clearly paraphyletic genus. Since many of the other species assigned to *Apseudes* are recorded from the deep-sea, or from distant locations, we here only compare our species with those previously assigned to *Muramurina* and *Androgynella*, as well as warm-water American species of *Apseudes*. For comparison see Table 2.

Etymology. The name reflects Fernando de Noronha Island where the species was collected.

Apseudes aisoe **n. sp**.

(Figures 26–28)

Material examined. Holotype: simultaneous hermaphrodite with female cheliped morphology and oostegites (Reg. Nº MOUFPE 14.286), 5.4 mm. Station NE IV #178, 3rd December 2000, coordinates: 11°27´S 37°02´W. Sergipe State (SE), Brazil; water depth 71.6 m.

Paratypes: one simultaneous hermaphrodite with oostegites and male cheliped morphology (dissected) (Reg. Nº MOUFPE 14.287), 4.7 mm. One simultaneous hermaphrodite with oostegites and female cheliped morphology (dissected) (Reg. Nº MOUFPE 15.067). Same locality as the holotype. Thirteen specimens simultaneous hermaphrodite (damaged) (Reg. Nº MOUFPE 15.045); same locality as the holotype. Two simultaneous hermaphrodites with oostegites (Reg. Nº MOUFPE 14.288); station NE IV #181, 4 December 2000, coordinates: 11°90´S 37°40´W. Bahia State (BA), Brazil; water depth 40.5 m. Eighteen simultaneous hermaphrodites (11 damaged) (Reg. Nº MOUFPE 14.289); station NE IV #176, 3 December 2000, coordinates: 10°66´S 36°23´W. Alagoas State (AL), Brazil; water depth 71.2 m. One simultaneous hermaphrodite with oostegites (Reg. Nº MOUFPE 14.290); station NE I #243, 24 October 1995, coordinates: 09°17´S 34°91´W. Alagoas State, Brazil; water depth 51 m. Holotype and all paratypes were collected in muddy and sandy sediments, algae and sponges.

Diagnosis. Simultaneous hermaphrodite with oostegites. Pereonites 3–6 with lateral plumose setae; carapace without setae. Antenna with more than 15 articles. Maxilliped basis with three long simple setae and one spiniform seta on inner distal margin; article 2 of maxilliped palp with two spiniform setae on outer distal margin. Pereopods 1, 3 and 6 with evident ‘suture’ on ventroproximal to distal margin.

Description. Body from holotype, appendages from dissected paratype.

Body (Figure 26A, B): slightly calcified. Dorsoventrally flattened; about 4.5 times as long as wide. With plumose setae on lateral margins of pereonites 3–6. Cephalothorax: slightly longer than wide, naked, about 20% of total body length. Rostrum tip pointed. With two spiniform projections posterior to eye lobes. Ocular lobes and visual elements present. Pereon (Figure 26): about 52% of total body length, about 2.8 times as long as wide. Pereonites 1–5 with distinct hyposphenians on ventral margin. Pereonite 1 wider than each following pereonites, slightly longer than pereonite 2; with two simple setae on posterior lateral margins. Pereonite 2 with three simple setae on anterolateral margins and one pair of simple setae on posterior lateral margins. Pereonites 3–6 subequal, with short expansions on anterolateral margins; three-five plumose setae and one-two simple setae on anterior and posterior lateral margins, respectively. Pereonite 6 (Figure 26B) with ventral penal genital cone. Pleon: about 30% of total body length, about 1.3 times as long as wide; with three-five plumose setae on lateral margins of each pleonite. Pleotelson as long as three first pleonites combined, about 1.3 times as long as wide; with one pair of simple setae on lateral margins. All pleonites with pleopods and soft ventral keel.

Antennule (Figure 26C): peduncle article 1 about 1.3 times as long as cephalothorax, about 3.5 times as long as wide; inner margin with several proximal short spines, eight simple setae and two distal spines; outer margin with five proximal setulated setae, eight simple setae and one distal spine. Peduncle article 2 longer than each following article; with four simple setae on outer margin; six simple setae and three setulated setae on inner margin. Peduncle article 3 half as long as article 2; with four simple setae. Peduncle article 4 (common article) with four simple setae. Outer flagellum of 13 serially repeating articles; with at least one or two simple setae. Articles 3, 6, 9 and 11 with one aesthetasc. Terminal article with three simple setae. Inner flagellum of seven serially repeating articles; with onethree simple setae on each article. Terminal article with five simple setae.

Antenna (Figure 27G): 16 articles, about 0.6 times as long as antennule. Article 1 broad, expanded internally; with one short spiniform seta and two simple setae on inner distal margin. Article 2 longest, as long as following two articles combined; inner margin with five proximal short and one distal spiniform setae, three proximal simple setae; one proximal simple seta and one distal simple seta on outer margin, with proximal scales. Squama as long as article 2; with nine simple setae. Article 3 short; with one long simple seta and one spiniform seta on inner distal margin. Article 4 longer than each following article, about 1.2 times as long as article 5; with one proximal simple seta and two distal setulated setae on inner margin. Article 5 with one medial simple seta; two simple setae and one setulated seta on inner distal margin; three setulated setae on outer distal margin. Articles 6–15 serially repeating; with one-four simple setae Article 11 with one aesthetasc. Terminal article with four simple setae.

Mouthparts (Figure 27A–F): labrum not recovered. Mandibles (Figure 27A, A1, B, B1, B2) molar typical for Apseudidae, long, broad with heavily chitinous apex (Figure 27A1, B2). Palp triarticulate about 8.5 times as long as wide. Article 1 shorter than other articles; with four simple setae. Article 2 about two times as long as article 1, 1.8 times as long as article 3; with one simple and 12 pinnate setae. Article 3 about 1.3 times as long as article 1; with 11 pinnate setae and one long terminal pinnate seta. Left mandible (Figure 27A) incisor and lacinia mobilis well developed; with four and five denticles, respectively; setal row with five distal bifurcate setae arising from a common peduncle. Right mandible (Figure 27B, B1) incisor with four denticles; setal row with four distal bifurcate setae and one multifurcate seta arising from a common peduncle. Maxillule (Figure 27C, C1) palp biarticulate, terminal article with five distal serrated setae; outer endite with several fine setae on inner and outer margins, nine distal spiniform setae and two bipinnate setae on ventral margin; inner endite with five distal circumplumose setae. Maxilla (Figure 27D) outer lobe of movable endite with four distal bipinnate setae; inner lobe of movable endite with two bipinnate setae and one spiniform seta on distal margin; outer lobe of fixed endite distal margin with four complex setae and four bipinnate on ventral margin; inner lobe of fixed endite with row (25–30) of bipinnate setae, distal margin with 7-8 stout bipinnate setae; inner and outer basal margins with several fine simple setae. Maxilliped (Figure 27E, E1) basis about 1.2 times as long as wide; with one spiniform seta and three long simple setae on inner distal margin. Endite (Figure 27E1) distal margin with eight complex setae; three coupling hooks on ventral margin and two spiniform setae on outer distal margin; nine circumplumose setae on inner margin. Palp article 1 as long as article 3; with one simple seta on inner distal margin and one spiniform seta on outer distal margin. Article 2 about 1.2 times as long as articles 3 and 4 combined; with several simple setae on inner margin; two spiniform setae on outer distal margin. Article 3 with 13 simple setae on inner margin. Article 4 with four pinnate setae and eight simple setae on ventral margin; one setulated seta on outer distal margin. Epignath (Figure 27F) cup-shaped, terminal seta stout and circumplumose.

Cheliped (Figure 26D, E): **male form** (Figure 26D): robust, exopod triarticulate with four distal plumose setae. Basis stout, about 1.4 times as long as wide; ventral margin with three proximal simple setae, one medial stout spiniform seta and four distal simple setae. Merus with three simple setae on dorsal margin; one spiniform seta and four simple setae on ventral margin. Carpus about 1.7 times as long as wide; carpus ventral margin shorter relative to the length of the propodus; with three dorsal simple setae and five simple setae on ventral margin. Propodus as long as basis, about 1.2 times as long as wide; with one serrated seta and four simple setae next to insertion of dactylus. Fixed finger with evident expansion (common in male), and three simple setae (which one is longer) on proximal inner margin; ten simple setae on inner and ventral margins. Dactylus slightly longer than fixed finger; with five denticles on inner margin and two dorsodistal simple setae. **Female form** (Figure 26E): as male cheliped except for exopod with five distal plumose setae. Basis about 1.7 times as long as wide; with one proximal short spiniform seta and one distal simple seta on ventral margin. Merus with one strong seta on dorsodistal margin; one distal spiniform seta (broken) and two simple setae on ventrodistal margin. Carpus ventral margin wider than male cheliped and straight laterally; with two simple setae on dorsal margin and six simple setae on ventral margin. Propodus with five simple setae on dorsodistal margin and three next to insertion of dactylus; two short spiniform setae and three simple setae on ventral margin. Fixed finger with six simple setae on ventral margin; six simple setae on inner margin. Dactylus with three simple setae on dorsodistal margin; five denticles on inner margin.

Pereopod 1 (Figure 28A): not illustrated at same scale to other pereopods. Fossorial type. Coxa with prominent apophysis and three distal simple setae (not illustrated). Exopod triarticulate with six plumose setae. Basis about 2.6 times as long as wide, with distinct suture from proximal to distal margin; ventral margin with two proximal, two medial and five distal simple setae, and one distal spiniform seta; two medial simple setae and one distal seta on dorsal margin. Ischium with three ventrodistal simple setae. Merus longer than each following article; with four simple setae and one spiniform seta on dorsodistal margin; seven medial simple setae, four distal simple setae and one distal spiniform seta on ventral margin. Carpus as long as propodus; with 13 simple setae and one spiniform seta on dorsodistal margin; six simple setae and two spiniform setae on ventral margin.

Propodus approx. 1.1 times as long as dactylus and unguis combined; dorsal margin with two spiniform setae, three simple setae and one medial setulated seta; ventral margin with four spiniform setae, nine simple setae and one short pinnate seta next to insertion of dactylus. Dactylus with three ventromedial denticles and three dorsodistal simple setae. Unguis pointed and curved, about 35% of total dactylus and unguis combined length.

Pereopod 2 (Figure 28B): coxa with one simple and one setulated seta. Basis about 2.7 times as long as wide; one proximal setulated seta and one medial simple seta on dorsal margin; ventral margin with three proximal simple setae, two medial and three distal simple setae. Ischium with two ventral simple setae and one simple seta on dorsal margin. Merus as long as carpus; with three dorsodistal simple setae; ventral margin with two medial simple setae, two distal spiniform setae and two distal simple setae. Carpus about 0.7 times as long as propodus; with nine simple setae and one spiniform seta on dorsodistal margin; ventral margin with two medial simple setae and one spiniform seta, two distal simple setae and two spiniform setae. Propodus about 1.2 times as long as dactylus and unguis combined; with two spiniform serrated setae and four simple setae on dorsodistal margin; ventral margin with three spiniform serrated setae and one spiniform seta, three simple setae and one short pinnate seta. Dactylus with two denticles on ventral margin and one pair of simple setae on dorsomedial margin. Unguis shape as in pereopod 1, about 40% of total lengths of dactylus and unguis combined.

Pereopod 3 (Figure 28C): coxa with two setulated setae. Basis with evident suture from proximal to distal margin; with one proximal plumose seta and six simple setae on dorsal margin; six ventrodistal simple setae. Ischium with three ventrodistal simple setae and two simple setae on dorsodistal margin. Merus as long as carpus; with two dorsodistal simple setae; ventral margin with three medial simple setae, two simple setae and two spiniform setae distally. Carpus about 0.8 times as long as propodus; with six simple setae and one spiniform seta on dorsodistal margin; ventral margin with one medial spiniform seta and two simple setae, two distal spiniform and two simple setae. Propodus as long as dactylus and unguis combined; with three spiniform setae and three simple setae on dorsodistal margin; ventral margin with one proximal, two medial and one distal spiniform setae, one simple and one short pinnate seta. Dactylus as in pereopod

2. Unguis shape as in pereopod 1, about 47% of total lengths of dactylus and unguis combined.

Pereopod 4 (Figure 28D): basis about 2.6 times as long as wide; with three simple setae and one plumose seta on ventroproximal margin, one ventrodistal simple seta. Ischium with three ventrodistal simple setae and one dorsodistal simple seta. Merus about 0.6 times as long as carpus; with one dorsodistal simple seta; three ventromedial simple setae, one pair of spiniform setae and another pair of simple setae on ventrodistal margin. Carpus about 1.3 times as long as propodus; with two simple setae and three spiniform setae on dorsodistal margin; ventral margin with two medial spiniform setae, one distal simple seta and four spiniform setae. Propodus about 1.7 times as long as dactylus and unguis combined; with one dorsomedial setulated seta, a row of short pinnate setae and two serrated setae slightly longer than dactylus on dorsodistal margin; one spiniform seta and one simple seta on ventromedial margin, one pinnate seta and two spiniform setae on ventrodistal margin. Dactylus and unguis combined shorter than other pereopods, dactylus with two ventromedial denticles and one dorsomedial simple seta. Unguis shape as in pereopod 1.

Pereopod 5 (Figure 28E): basis about 3.2 times as long as wide; dorsal margin with one proximal setulated seta, one medial simple seta and two plumose setae; ventral margin with three proximal plumose setae and one simple seta, two medial plumose setae and four distal simple setae. Ischium with two dorsodistal simple setae and three ventrodistal simple setae. Merus as in pereopod 4 except for having six ventral simple setae. Carpus as long as propodus; with three plumose setae and one simple seta on dorsalmargin; ventralmargin with two proximal and three distal spiniform setae, and two distal simple setae. Propodus about 1.1 times as long as dactylus and unguis combined; with one dorsomedial setulated seta, two spiniform and two simple setae on dorsodistal margin; ventral margin with two medial and two distal spiniform setae, and a row of short pinnate setae. Dactylus with two ventrodistal denticles and three dorsomedial simple setae. Unguis as in pereopod 2.

Pereopod 6 (Figure 28F): basis with distinct suture as in pereopods 1 and 3; with two setulated setae on ventroproximal margin, nine and eleven plumose setae on dorsal and ventral margins, respectively. Ischium with one plumose and one simple seta on dorsodistal margin; one ventrodistal tiny simple seta. Merus about 0.8 times as long as carpus; with five dorsal plumose setae; one spiniform, one plumose and five simple setae on ventral margin. Carpus as long as propodus; with seven dorsal plumose setae; one plumose and six simple setae on ventral margin. Propodus as long as dactylus and unguis combined; with one setulated seta, about seven pinnate and two spiniform setae on dorsodistal margin; two proximal spiniform setae and row of pinnate setae (45–50) on ventral margin. Dactylus with two denticles and one simple seta on ventral margin; one dorsomedial simple seta. Unguis as in pereopod 2.

Pleopods (Figure 26F): basal article biarticulate; with four plumose setae. Endopod with about 21 plumose setae. Exopod with about 20 plumose setae.

Uropods (Figure 26G): basal article short, apparently naked. Exopod with nine subequal articles; with one and two simple setae on articles 2 and 3, respectively; article 5 with one long simple seta as long as each following article, terminal article with five simple setae. Endopod partly damaged, with about 17 subequal articles; with one-two simple setae on articles: 4–6, 8, 10, 12, 14 and 16.

Remarks. *Apseudes aisoe* n. sp. shares some features with *A. curtiramus* (Guţu, 2007a) and *A. fagettii* (Báez & Magnere, 1980) mainly by the type of seta(e) on inner margin of article 2 of the maxilliped palp and the type of seta(e) of the antenna squama. However, *A. aisoe* can be separated from these species by having: (1) three long simple setae and one spiniform seta on inner distal margin of the maxilliped basis (one plumose seta in *A. fagettii* and one medial simple seta in *A. curtiramus*); (2) two long spiniform setae on outer distal margin of article 2 of maxilliped palp (one shorter in *A. fagettii* and *A. curtiramus*); (3) a 'suture' on the ventroproximal margin of pereopods 1, 3 and 6 (absent in other species of *Apseudes*); and (4) 16 articles on the antenna (ten in *A. fagettii* and 13 in *A. curtiramus*).

By comparison of the paratype with the holotype, it was observed that the number of the antennule articles in the outer and inner flagellum varied. While the numbers in the paratype were 13/7 articles (outer and inner flagellum, respectively), 17/9 articles were observed for the holotype. This variation might be the result of a re-growth or an intraspecific variation and, thus, is not suitable as a diagnostic character alone.

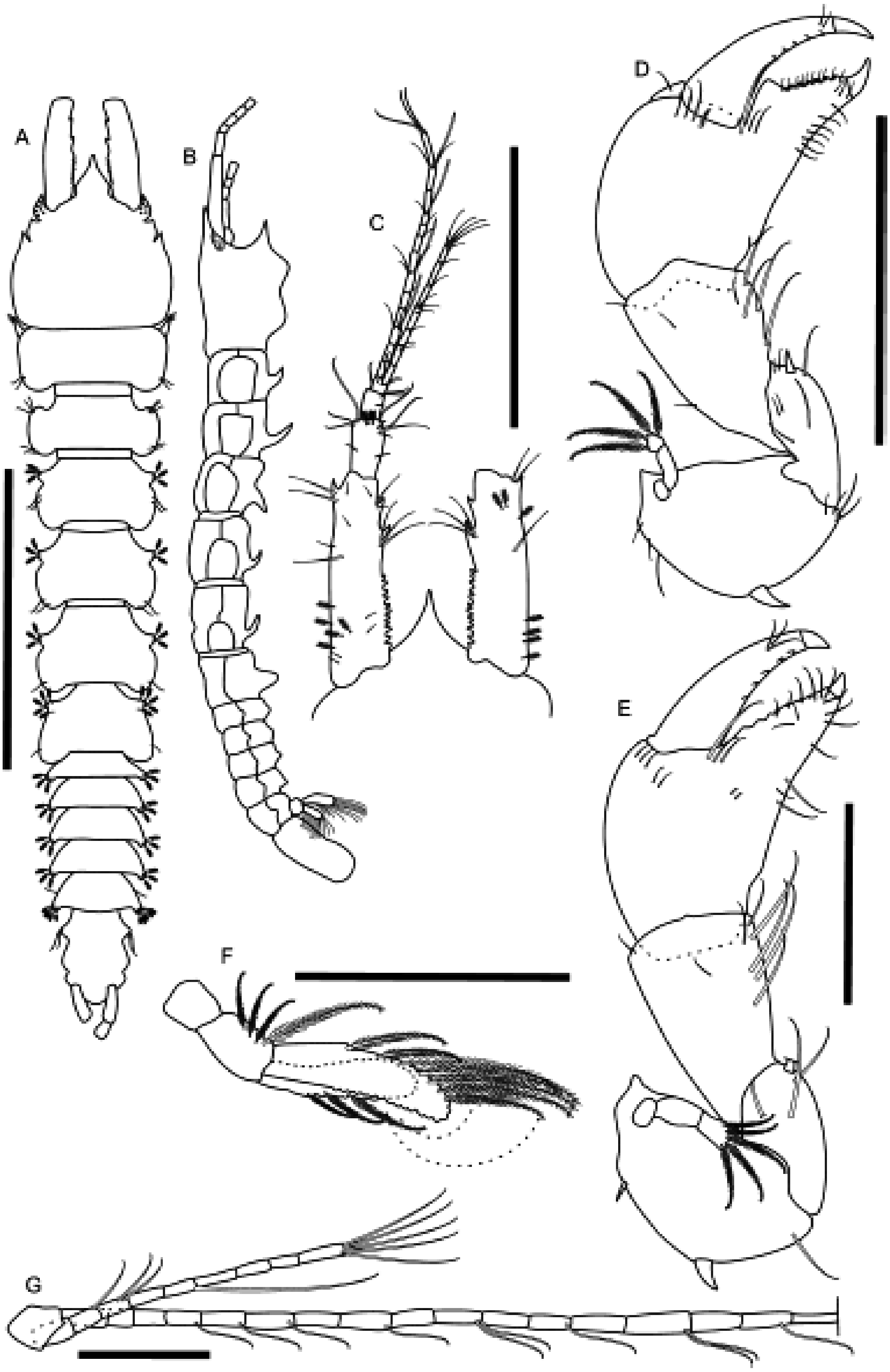


Figure 26. *Apseudes aisoe* n. sp., simultaneous hermaphrodite. Holotype (Reg. Nº MOUFPE 14.286): (A), dorsal view; (B), lateral view. Paratypes (Reg. Nº MOUFPE 14.287 and Reg. Nº MOUFPE 15.067): (C), antennule; (D), cheliped male form; (E), cheliped female form; (F), pleopod; (G), uropod. Scale bars: (A–C), 1 mm; (D-F), 0.5 mm; (G), 0.2 mm.

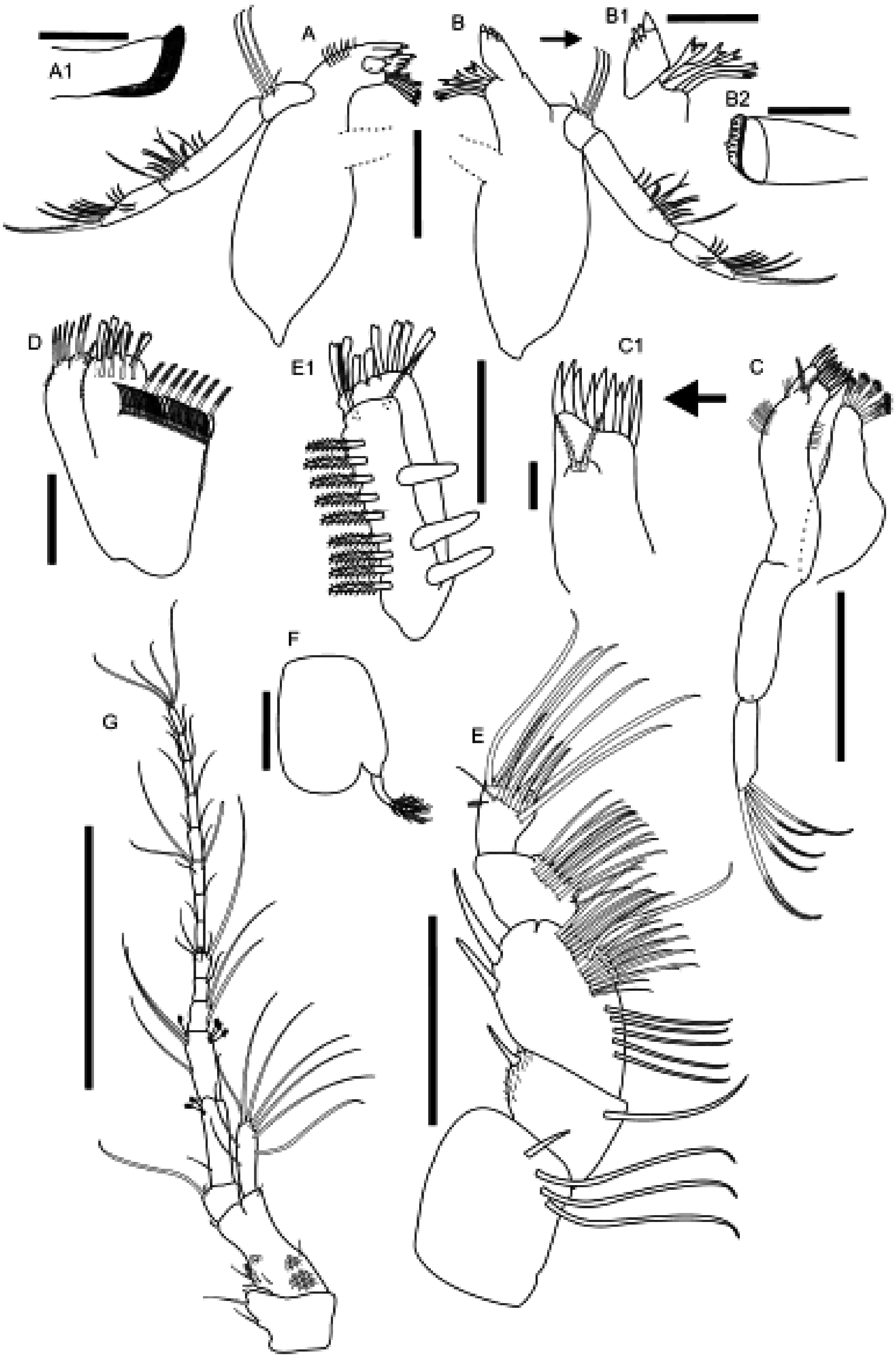


Figure 27. *Apseudes aisoe* n. sp., simultaneous hermaphrodite. Paratype (Reg. Nº. MOUFPE 14.287). (A), Left mandible; (A1), molar process of left mandible; (B), right mandible; (B1), detail of incisor of right mandible; (B2), molar process of right mandible; (C), maxillule; (C1), detail of outer endite of maxillule; (D), maxilla; (E), maxilliped; (E1), maxilliped endite; (F), epignath; (G), antenna. Scale bars: (A, B, C1, D–F), 0.2 mm; (A1, B1, B2, E1), 0.1 mm; (C, G), 0.5 mm.

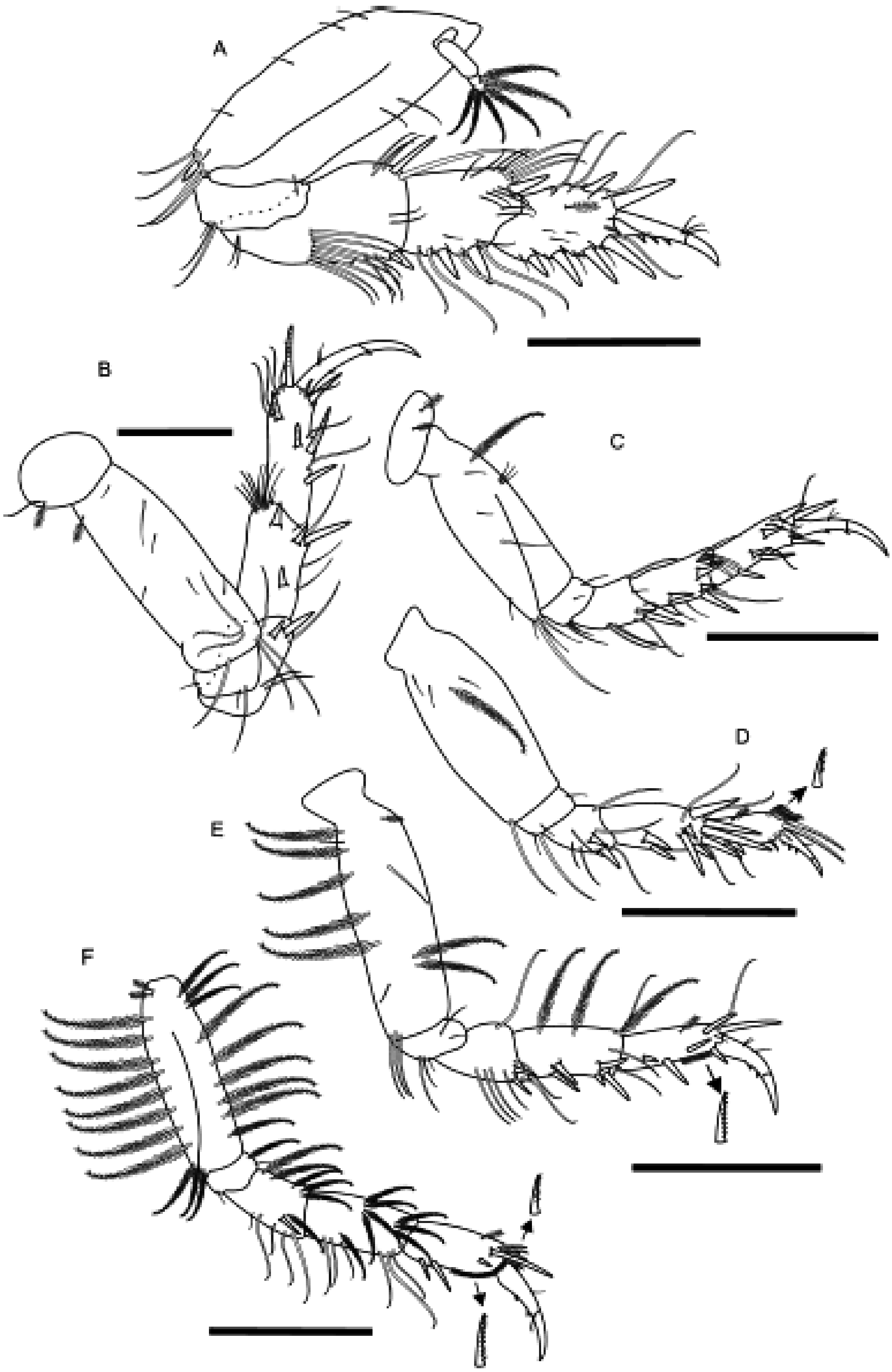


Figure 28. *Apseudes aisoe* n. sp., simultaneous hermaphrodite. Paratype (Reg. Nº. MOUFPE 14.287). (A), Pereopod 1; (B), pereopod 2; (C), pereopod 3; (D), pereopod 4; (E), pereopod 5; (F), pereopod 6. (A–F), Scale bars: 0.5 mm.

Specifically, we found specimens of *A. aisoe* that were both with oostegites and with a penal cone, but sexual variations in the cheliped morphology corresponding to what was recorded for *Apseudes talpa* and backed by genetic evidence (Larsen *et al*. 2011). We also found that, regardless of cheliped morphology, all examined specimens had a penal cone, even with oostegites. We dissected several specimens of both forms and all characters (body shape, appendages and mouthparts) were identical, except for the chelipeds. We have thus no hesitation about the conspecificity of our specimens despite differences in the cheliped morphology.

Etymology. The name ‘aisó’ is derived from the tupi-guarani language, and means ‘beautiful’.

Discussion

Large numbers of specimens of *Apseudes*, previously identified as *Muramurina* from the northeastern coast of Brazil, allowed a study of the diagnostic characters between the species of *Apseudes* and *Muramurina*.

Guţu (2006) separated the genera *Muramurina* (as *Muramura*) and *Androgynella* from *Apseudes* based mainly on the character of simultaneous hermaphroditism.

Guţu (2006: 84) described the difference between *Muramurina* and *Androgynella* as: size (9–16 mm in *Androgynella*, 4–5mm in *Muramurina*); the length ratio between the mandible palp articles as the article 2 about 1.5 times as long as article 3 in *Muramurina*, and, usually, at least 2 times as long as article 3 in *Androgynella*; the number of spiniform setae (‘spines’ in Guţu’s (2006) terminology) on the outer distal corner of article 2 of maxilliped palp (only one in *Muramurina*, and, usually, two or three in *Androgynella*); the presence of plumose setae on antennule peduncle article 1; presence of circumplumose setae on the anterolateral margins of the carapace (in *Androgynella*); and the presence of simple setae of the antenna squama in *Muramurina*, while circumplumose in *Androgynella*.

In table 2 we list the diagnostic characters, as given by Guţu (2006, 2007a), observed in all species formerly attributed to *Androgynella* and *Muramurina*. These observations reveal no consistent diagnostic characters (no synapomorphies) and, thus, force us to reject these genera. We here reconfirm that *Androgynella* is a junior synonym of *Apseudes* and suggest that *Muramurina* also should be synonymised with *Apseudes*. A similar argument was raised by Bamber (2012: 1102).

Acknowledgements

The authors would like to honour the recently deceased Dr. Petrônio Alves Coelho (Universidade Federal de Pernambuco, Museu de Oceanografia ‘Petrônio Alves Coelho’) in recognition of his many contributions to crustacean research in Brazil. The first author would also like to thank Dr. Luis Ernesto A. Bezerra (Universidade Federal Rural do Semi-Árido/UFERSA) for the support with the map of study area, and thanks are due to the criticism of the anonymous reviewers. This paper is part of a Ph.D. dissertation (CLAS) funded by CAPES — Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Grant number 5428/10-6).

References

Anderson, G. (2012). *Tanaidacea Classification*, February 2, 2012. Available online at http://peracarida.usm.edu/TanaidaceaTaxa.pdf: 1–30.

Araújo-Silva, C.L. & Larsen, K. (2010). Tanaidacea from Brazil. II. A revision of the subfamily Hemikalliapseudinae (Kalliapseudidae; Tanaidacea; Crustacea) using phylogenetic methods. *Zootaxa*, 2555: 30–48.

Araújo-Silva, C.L. & Larsen, K. (2012). Tanaidacea from Brazil. III. New records and description of a species collected from REVIZEE-NE Program. *Nauplius*, 20 (2): 87–105.

Báez, R.P. & Magnere, O.B. (1980). *Apseudes fagettii* nov. sp. de las Islas Juan Fernandez (Crustacea, Tanaidacea, Apseudidae). *Boletín del Museo Nacional de Historia Natural*, 37: 295–302.

Bamber, R.N. (2012). Littoral Tanaidacea (Crustacea: Peracarida) from Macaronesia: allopatry and provenance in recent habitats. *Journal of the Marine Biological Association of the United Kingdom*, 92 (5): 1095–1116.

Błazewicz-Paszkowycz, M. & Larsen, K. (2004). Three new deep-sea species of Apseudidae (Tanaidacea; Apseudomorpha) from the southern seas and Antarctica. *Crustaceana*, 77 (4): 467–498.

Dana, J.D. (1849). Conspectus Crustaceorum, Conspectus of the Crustacea of the U.S. Exploring Expedition. *American Journal of Science and Arts, (2),* 8: 424–428.

Guţu, M. (2002). Contributions to the knowledge of the genus *Apseudes* Leach, 1814. (Crustacea:Tanaidacea, Apseudomorpha) from the Mediterrane Basin and North African Atlantic. *Travaux du Muséum d'Histoire Naturelle 'Grigore Antipa*', 44: 19–39.

Guţu, M. (2006). *New apseudomorph taxa of the world ocean: Crustacea, Tanaidacea*: 1–318. (Curtea Veche, Bucharest).

Guţu, M. (2007a). Contribution to the knowledge of the Indo-West-Pacific Apseudomorpha (Crustacea: Tanaidacea). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'*, 50: 47–86.

Guţu, M. (2007b). *Muramurina*, a new name for *Muramura* Guţu, 2006 (Tanaidacea Apseudoidea) preoccupied by *Muramura* Pledge, 1987 (Mammalia: Diprotodontia: Vombatoidea). *Journal of Crustacean Biology*, 27 (3): 520.

Guţu, M. (2008). New data on the genus *Paradoxapseudes* Guţu, 1991, including the description of a new species. The synonymysation of *Gollumudes* Bamber, 2000 with *Paradoxapseudes* and the description of a new apseudid genus (Crustacea: Tanaidacea). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'*, 51: 17–42.

Guţu, M. & Iliffe, T.M. (1989). *Apseudes orghidani*, a new species of Tanaidacea (Crustacea) from an anchialine cave on Bermuda. *Travaux du Muséum d'Histoire Naturelle 'Grigore Antipa',* 30: 161–167.

Lang, K. (1953). *Apseudes hermaphroditicus* n. sp. a hermaphroditic tanaid from the Antarctic. *Arkiv för Zoologie*, 2: 341–350.

Larsen, K. (2003). Proposed new standardized terminology for tanaidacean Crustacea. *Journal of Crustacean Biology*, 23 (3): 644–661.

Larsen, K. (2005). *Deep-sea Tanaidacea (Peracarida) from the Gulf of Mexico*. Crustaceana Monographs, 5: i-x, 1–381. (Brill, Leiden).

Larsen, K. (2006). Tanaidacea (Crustacea; Peracarida) from chemically reduced habitats the hydrothermal vent system of the Juan de Fuca Ridge, Escabana Trough and Gorda Ridge, northeast Pacific. *Zootaxa*, 1164: 1–33.

Larsen, K., Bertocci I. & Froufe E. (2011). *Apseudes talpa* revisited (Crustacea; Tanaidacea). The impact on apseudidaen systematics. *Zootaxa*, 2886: 19–30.

Larsen, K. & Shimomura, M. (2006). Tanaidacea (Crustacea: Peracarida) from Japan. I. Apseudomorpha from the East China Sea, Seto Island Sea, and Nansei Islands. *Zootaxa*, 1341: 29–48.

Leach, W.E. (1814). *Crustaceology*. *In:* Brewster, D. (ed.), The Edinburgh Encyclopedia: 383–437.

Holme, N.A. & Mcintyre A.D. (1984). *Methods for the study of marine benthos*, 2: 1–387. (Blackwell, London).

Montagu, G. (1808). Description of several animals found on the south coast of Devonshire. *Transactions of the Linnean Society of London*, 9: 81–114.

Shiino, S.M. (1937). On *Apseudes nipponicus* n. sp. (Crustacea Tanaidacea). *Annotationes Zoologicae Japonenses*, 16: 53–62.

Shiino, S.M. (1963). Tanaidacea collected by Naga Expedition in the Bay of Nha-Trang, South Viet-Nam. Report of the Faculty of Fisheries, Prefectural University of Mie, 4: 437–507.

Shiino, S.M. (1978). [Published 1979.] Tanaidacea collected by French scientists on board the survey ship 'Marion-Dufresne' in the regions around the Kerguelen Islands and other subantarctic islands in 1972, '74, '75, '76. *Science Report of Shima Marineland*, 5: 1–122.

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzeiger*, 205: 401–416.

Studer, T. (1884). Isopoden, gesammelt während der Reise S.M.S Gazelle um die Erde, 1874–76. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 1884: 1–28.

DOI:10.1163/15685403-00003155

Journal of the Marine Biological Association of the United Kingdom, Marine Biological Association of the United Kingdom, 94 (5): 969–974 (2014).

Article 4. A new genus of Colletteidae (Crustacea: Peracarida: Tanaidacea) from the Pacific with comments on dimorphic males with species specific characters

Kim Larsen[1] & Catarina L. Araújo-Silva[1,2]

[1]CIMAR/CIIMAR (Centro Interdisciplinar de Investigacão Marinha e Ambiental), AEE (Aquatic Ecology and Evolution), Rua dos Bragas 289, 4050-123 Porto, Portugal, [2]Capes Foundation, Ministry of Education of Brazil, Brasília–DF, 70040–020, Brazil

Abstract

A new genus and species of Tanaidacea are described from the manganese nodule province between the Clarion and the Clipperton Fracture Zone of the equatorial North Pacific Ocean collected during the French/German BIONOD expedition in 2012. The new genus, *Cheliasetosatanais*, can be diagnosed by the propodal and dactylus setation and the maxilliped endite armament. The male is also described and, while being a dimorphic swimming male, still shares the diagnostic characters and posseses a fully functional maxilliped.

Key words: Tanaidacea, Tanaidomorpha, manganese nodule province, BIONOD cruise, dimorphic males

Introduction

This is the third paper in a recent series on the tanaidacean assemblage in the Central Pacific Manganese Nodule Province. The two recent papers centred on the genera *Collettea* (G.O. Sars, 1882), *Robustochelia* Kudinova-Pasternak, 1983 and *Tumidochelia* Knight *et al*., 2003 (Larsen 2011a) and *Stenotanais* Bird & Holdich, 1984 and *Typhlotanais* G.O. Sars, 1882 (Larsen 2011b). Previous papers of the tanaidacean fauna from this general area have dealt with the genera

Agathotanais Hansen, 1913 (Larsen 1999) and *Collettea* (G.O. Sars, 1882) (Larsen 2000).

This paper deals with a new genus, but, more importantly, it deals with the identification of dimorphic males and their assignment to females of a given species (see Larsen 2002). The identification of dimorphic- of even polymorphic males and assignment to their respective females, have been a long standing problem for tanaid systematics (Larsen & Wilson 2002; Guerrero-Kommritz & Brandt 2005; Bird & Larsen 2009) but some shared species-specific characters might be present and this topic should be investigated further in other taxa.

Materials and Methods

Samples were taken during the French/German BIONOD expedition between 28 April and 11 May 2012, from aboard the research vessel 'L´Atalante' using epibenthic sledges. The material was sieved through 0.5 and 0.3 mm mesh. Parts of the material were fixed and stored in 96% alcohol for genetic treatment.

Dissections were made in glycerin using chemically sharpened tungsten wire needles. Body length was measured from the tip of the cephalothorax to the apex of the pleotelson. The terminology in the descriptions is based on Larsen (2003), although the minute terminal article of the antennule is here termed 'terminal cap-like article' (see Larsen *et al.* 2013). Adjectives such as *long* and *short* are used as relative qualifiers in respect of the appendage being described. Types are deposited in the Museum National d'Histoire Naturelle Paris (MNHN).

Systematics

Order TANAIDACEA Dana, 1849

Suborder TANAIDOMORPHA Sieg, 1980

Superfamily PARATANOIDEA Lang, 1949

Family COLLETTEIDAE Larsen & Wilson, 2002

Cheliasetosatanais **n. gen**.

Diagnosis. Female: pereon composed of six free pereonites, pleon composed of five free pleonites with small ventral apophyses and pleotelson. Antennule with five articles of which the terminal article is minute and cap-like. Antenna with six articles. Labrum with distal setae of a robust nature. Mandible incisor and lacinia mobilis well calcified; molar wide with distal denticles but apex tapering and weakly calcified. Labium composed of two lobes with distal setae of a robust nature and with small inner spines. Maxilliped basis fused, with long lateral seta reaching midlenght on palp article 3; endites not fused, with three spiniform and outer and inner simple setae; palp article 3 with row of small outer spines. Cheliped attached via triangular sclerite; propodus with inner row of multiple robust setae; dactylus with inner cluster of setules and seta. Pereopodal propodi all with ventral spines. Pereopods 4–6 dactylus and unguis not fused. Pleopods absent. Uropodal endopod and exopod both composed of two articles. **Male:** swimming type. Pereon reduced; pleon enlarged; pleotelson with long (half the total length of pleotelson) apical spiniform process. Antennule with seven article plus terminal cap-like article; article 4–6 with ventrodistal cluster of aesthestascs. Mandibles absent. Maxilliped well developed; endite as in female; palp without spines and with simple setae only. Cheliped setation as in female. Pereopods 1–3 elongated and stick-like. Pleopods biramous. Uropod endopod triarticulated (first one pseudoarticulated), exopod bi-articulated.

Type-species. *Cheliasetosatanais spinimaxillipedus* n. sp.
Etymology. Named after the setose propodal cheliped.
Gender. Masculine.

Remarks. The male shows several similarities with the male of *Siphonolabrum* Lang, 1972 like the fully developed maxilliped, a heavy cheliped propodal and dactylar setation, and tri-articulated uropodal endopod but lacks the elongated labrum of *Siphonolabrum*. However, the female of the new genus clearly does not belong to the Anarthruridae Lang, 1971 on the basis of the mandibles, maxilliped endite armament, cheliped attachment, and biramous uropods. The male differs also from *Siphonolabrum* maxilliped endite armament and the bi-articulated uropodal exopod.

The male morphology deserves closer attention. Tanaidacean males are infamous for their different expression of morphology. Firstly there is the ‘female-looking’ type, as found in Agathotanaidae Lang, 1971, Tanaellidae Larsen & Wilson, 2002, *Parafilitanais* Kudinova-Pasternak, 1983, *Pseudoanarthrura* Larsen, 2005 and *Collettea* (G.O. Sars, 1882), where the male shares the female morphology except a thicker antennule (without multiple aesthestascs) and the presences of pleopods but retains functional mouthparts. Then there is the 'Tanaoidea-type', where the male also retains functional mouthparts but differs in the shape of the cephalothorax and chelipeds. Thirdly there are the 'Leptocheliidae-type', where the antennules contain multiple articles with bundles of aesthestascs, reduced mouthparts, heavily modified chelipeds but with the pereon/pleon only moderately modified. The fourth type is the typical 'swimming-male' found in Leptognathiidae, Paratanaidae Lang, 1949, Pseudotanaidae Sieg, 1976, and Typhlotanaidae Sieg, 1986 where the antennules contain multiple bundles of aesthestascs, reduced mouthparts, and all somites heavily modified but with a cheliped which displays only minor modifications. In this study we are faced with a fifth type, represented by the new genus and *Siphonolabrum* Lang, 1971 (Sieg 1986) which resemble the typical 'swimming-male', but with a fully developed maxilliped almost identical to that of the female. Since the new genus and *Siphonolabrum* clearly do not belong to the same family, the character of this male morphology is already homoplastic.

The identification of dimorphic males and their assignment to females of a given species have generally been considered close to impossible without application of genetic methods (Larsen 2001; Larsen & Froufe 2010, 2013). This is because the genders were considered to share no species-specific characters (Bird & Larsen 2009). However, as stated above, both the male of the new genus and that of *Siphonolabrum*, share some specific features with those of the female. For example, in the genus described herein, both the maxilliped endite armament, the strange cheliped setation, and to a lesser degree, similarities in the pointed pleotelson. In *Siphonolabrum* the genders share the enlarged labrum and the maxilliped morphology with the female (Sieg 1986: 144, fig. 96). It is entirely possible that some species-specific characters have been overlooked in the male of some of the other tanaid taxa known to harbour di- or polymorphic males (Leptocheliidae, Leptognathidae, Nototanaidae, Paratanaidae, Pseudotanaidae, Typhlotanaidae). It is here recommended that special attention should be taken when dealing with such taxa in the future.

Also of interest is the presence of a single prominent penial cone (albeit with two genital openings) on the male. Usually the single cone is restricted to the suborder Apseudomorpha, but has previously been recorded for a few species of tanaidomorphans (Kakui *et al*. 2011).

The genus fits with the family diagnosis of Colletteidae and is currently placed herein. However, few will dispute that the diagnosis of Colletteidae is too wide and that the family is not monophyletic. A phylogenetic analysis of the Colletteidae is, however, not within the scope of this study.

Cheliasetosatanais spinimaxillipedus **n. sp.**

(Figures 29–32)

Material examined. Holotype: adult female, station BIO12-06EBS, epi, 2 April 2012; coordinates: 11842.76′N 116840.35′W; water depth: 4261 m, 11846.22′N 116841.13′W, water depth: 4259 m.

Paratypes: one female, same locality, dissected. Two non-ovigerous females (one dissected). Two males (one dissected), same location.

Diagnosis. Currently like the generic diagnosis.

Etymology. Named after the spiniform setae on the maxilliped endites of both genders.

Description. Non-ovigerous female, 6.1 mm (Figures 29 and 30).

Body (Figure 29A, B): long and slender, 9.5 times as long as wide. Cephalothorax (Figure 29A): as long as first two pereonites combined, eyes and eye-lobes absent. Pereon (Figure 29A, B): pereonites with distinct lateral shield. Pereonites 1–3 widest anteriorly, pereonite 4 and 5 widest at midlenght, pereonites 5 and 6 widest posteriorly. Pereonite 1 shortest. Pereonite 6 marginally longer than pereonite 1 and shorter than 2. Pereonite 5 longest and marginally longer than pereonite 4. Pereonite 2 longer than pereonite 6 and shorter than pereonite 3. Pleon (Figure 29A, B): pleonites of equal length, all pleonites with small apophyses. Pleotelson: longer than three last pleonites combined. Apex pointed.

Antennule (Figure 29C, C1). Shorter than cephalothorax. Article 1 longest but shorter than rest of antennule, with one distal simple seta. Article 2 longer than article 3, apparently naked. Article 3 longer than wide, with one simple distal seta. Article 4 almost as long as article 2 and 3 combined, with two terminal setae of which one is almost as long as article. Article 5 (Figure 29C1), minute and cap-like partly covered by article 4, with one aesthetasc, one short and two long terminal setae almost as long as article 5.

Antenna (Figure 29D, D1) about 0.8 times as long as antennule, composed of six articles. Article 1 short and fused to the cephalothorax, naked. Article 2 elongated and widening dorsodistally, longer than article 3, with robust dorsodistal seta. Article 3 square, with robust dorsodistal seta. Article 4 longest, with one simple and two setulate distal setae. Article 5 longer than article 2, with one long distal seta. Article 6 (Figure 29D1) minute, with abrupt decrease in width midlenght, with two short setae midlenght and two long terminal setae.

Mouthparts (Figures 29E–G and 30A–E): labrum (Figure 29E) with distal setules and setae of a robust nature. Mandibles (Figure 29F, G) well-developed, molars wide but tapering, apex with distal denticles but weakly calcified. Left mandible (Figure 29F) incisor weakly bifurcated, with two small outer denticles, very heavily calcified; *lacinia mobilis* widening distally, with serrated apex, very heavily calcified. Right mandible (Figure 29G) incisor widely but unevenly bifurcated, very heavily calcified. Labium (Figure 30A) composed of two triangular lobes with distal setules and setae of a robust nature, with small inner spines. Maxillule (Figure 30B, C): endite with nine terminal spiniform setae, shaft with evenly spaced row of setules; palp with two long terminal setae. Maxilla (Figure 30D): ovoid, naked. Maxilliped (Figure 30E): basis fused, with long lateral seta; endites not fused, with a row of setules, three spiniform and outer and inner simple setae. Palp article 1 naked; article 2 with one outer and four inner bipinnate setae; article 3 with four bipinnate inner setae, with row of small outer spines; article 4 with five bipinnate terminal setae. Epignath not recovered.

Cheliped (Figure 30F, G): basis attached to cephalothorax via large sclerite, with dorsodistal seta. Merus triangular, with one ventral seta. Carpus longer than wide, no carpal shield, with two ventral setae and one small dorsal seta in each end. Propodus more than twice as long as wide, with inner vertical row of 12 robust setae increasing in length ventrally. Fixed finger with two ventral and three inner simple setae. Dactylus as long as fixed finger, with inner medial cluster of multiple setules (Figure 30G) and one dorsodistal seta.

Pereopod 1 (Figure 30H): coxa discrete (not illustrated). Basis long (more than 5.5 times longer than wide), naked. Ischium with one simple seta. Merus twice as long as wide, with one spiniform ventrodistal seta. Carpus longer than merus, with three spiniform distal setae. Propodus longer than carpus, with multiple ventral and terminal spines, one serrated robust and one simple dorsodistal setae, and one spiniform ventrodistal seta. Dactylus naked. Unguis sharp, twice as long as dactylus.

Pereopod 2 (Figure 30I): as pereopod 1 except: ischium with one robust seta. Carpus with four spiniform distal setae.

Pereopod 3 (Figure 30J): as pereopod 2 except: dactylus with medial seta.

Pereopod 4 (Figure 30K): coxa incompletely fused to body. Basis wider than pereopods 1–3 (3.3 times longer than wide), naked. Ischium short, with two simple setae. Merus with two unequally long spiniform ventrodistal setae. Carpus shorter than merus, with one bone-shaped and four distal spiniform setae. Propodus longer than merus, with one dorsomedial setulate seta, one spiniform dorsodistal and two spiniform ventrodistal setae, ventral margin with multiple spines. Dactylus naked, longer than unguis.

Pereopod 5 (Figure 30L): as pereopod 4 except: basis with one ventromedial setulate seta. Dactylus with small terminal setules.

Pereopod 6 (Figure 30M): as pereopod 4 except: propodus without dorsomedial setulate seta, with three spiniform dorsodistal and two ventrodistal setae, with multiple ventral and terminal spines. Dactylus with small terminal setules.

Pleopods: absent in female.

Uropods (Figure 30N): biramous. Basal article very wide, almost square. Endopod bi-articulated, article 1 as long as article 2, with one setulate distal seta; article 2 setation broken but with at least one subdistal and three terminal

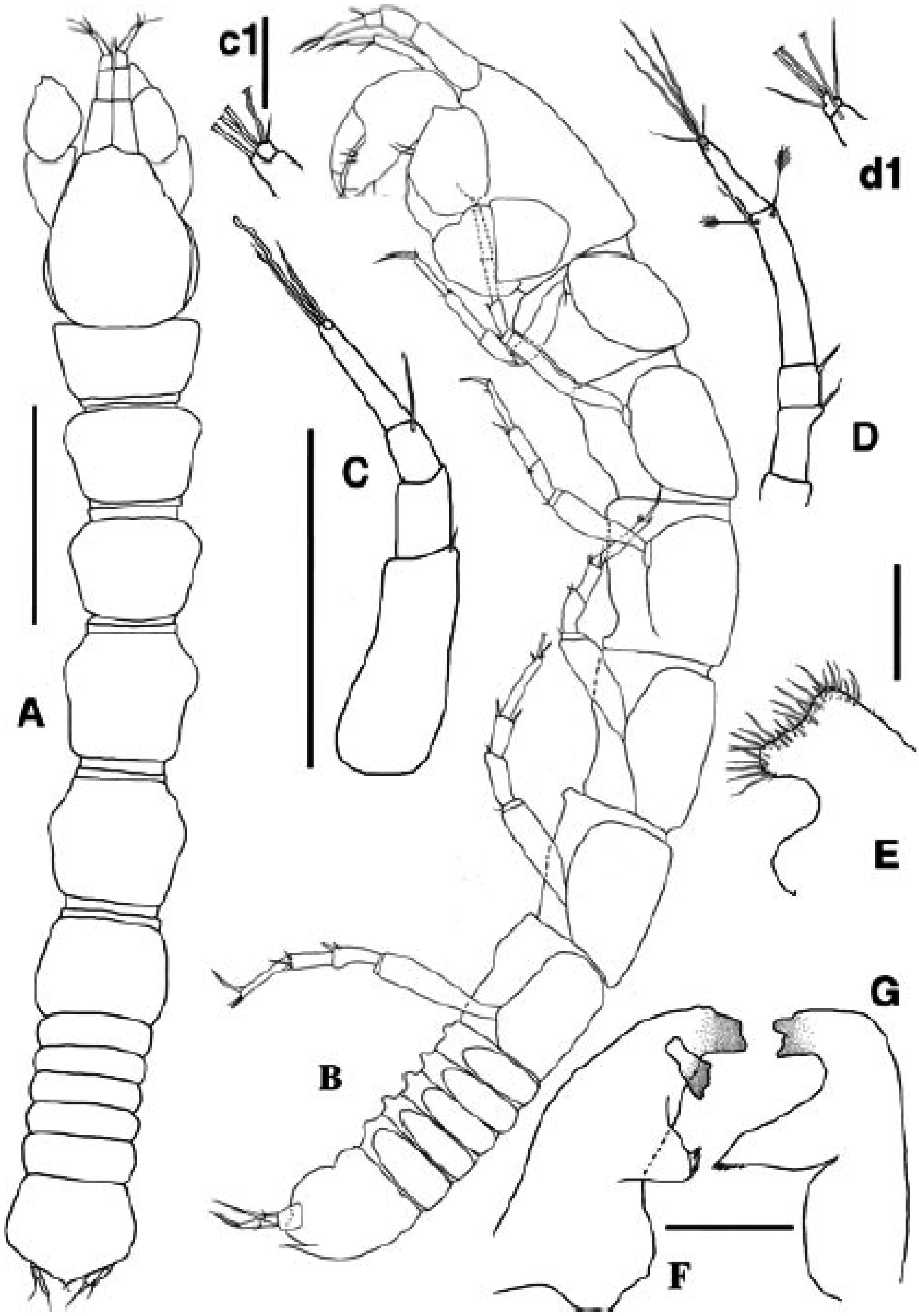


Figure 29. *Cheliasetosatanais spinimaxillipedus* n. sp., adult female: (A) holotype habitus dorsal view; (B) holotype habitus lateral view; female paratype: (C) antennule; (C1) same apex; (D) antenna; (D1) same apex; (E) labrum dorsal view; (F) left mandible; (G) right mandible. Scale bars: (A, B), 1 mm; (C, D), 0.5 mm; (E–G), 0.1 mm.

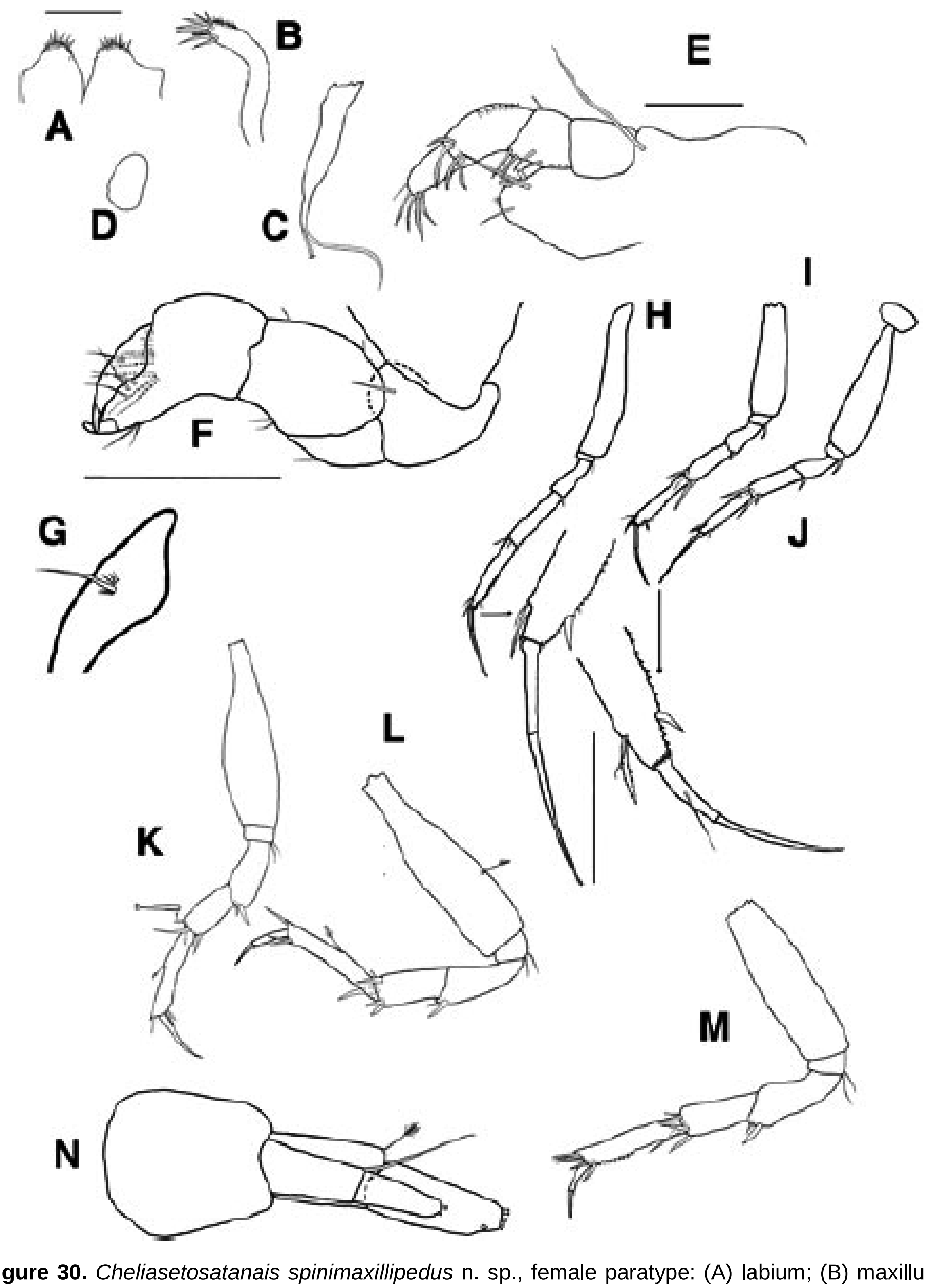


Figure 30. *Cheliasetosatanais spinimaxillipedus* n. sp., female paratype: (A) labium; (B) maxillule endite; (C) same palp; (D) maxilla; (E) maxilliped; (F) cheliped, outer view; (G) inner side of cheliped dactylus; (H) pereopod 1; (I) pereopod 2; (J) pereopod 3; (K) pereopod 4; (L) pereopod 5; (M) pereopod 6; (N) uropod. Scale bars: (A–E), 0.1 mm; (F–N), 0.5 mm.

setae. Exopod bi-articulated, combined longer than endopod article 1, with one long distal seta; article 2 shorter than article 1, setation broken but with at least two terminal setae.

Male, 3.8 mm (Figures 31 and 32). Body (Figure 31A, B): 5.3 times as long as wide. Cephalothorax triangular, marginally longer than wide, as long as pereonites 1–2 combined, with small blunt rostrum. Pereonites with indistinct lateral shield. Pereonites 1 to 3 widest anteriorly, pereonite 4 widest at midlength, pereonites 5 and 6 widest posteriorly. Pereonite 1 shorter than pereonite 2. Pereonite 2 shorter than pereonite 3. Pereonite 3 shorter than pereonite 4. Pereonite 4 longer than pereonite 5. Pereonite 5 longer than pereonite 6. Pereonite 6 as long as pereonite 1, with one prominent penial cone having two genital openings. Pleon with large triangular hyposphenEans, wider than pleotelson and posterior part of pereon, with clear lateral shield but no setae. Pleotelson (Figure 31G) longer than last three pleonites combined, apex tapering into a long (more than half of total pleotelson length) spiniform projection, with one pair of apical simple setae.

Antennule (Figure 31C): longer than cephalothorax, of eight articles. Article 1 more than twice as long as article 2, with three proximal simple setae and distal setulate seta, ventral margin with denticles. Article 2 more than twice as long as article 3, with one distal setulate seta. Article 3 about half as long as article 2, with one dorso-subdistal seta. Article 4 narrow and band-shaped, with multiple (many more than illustrated) ventrodistal aesthestascs. Article 5 longer than article 3, with multiple ventrodistal aesthestascs. Article 6 as long as article 7, with multiple ventrodistal aesthestascs. Article 7 about as long as article 2, with one long seta (longer than article itself). Article 8 minute and cap-like, with one long and one short simple distal setae.

Antenna (Figure 31D): 0.75 times as long as antennule, of seven articles. Article 1 fused with cephalothorax and partly fused (pseudoarticulated) with article 2. Article 2 longer than article 3, widening distally and with one dorsal simple seta. Article 3 shorter than article 4, with dorsodistal seta. Article 4 half as long as article 6, with dorsodistal setulate seta. Article 5 twice as long as article 3, with five simple distal, and two setulate subdistal setae. Article 6 longer than article 5 with one long simple seta. Article 7 minute, with abrupt decrease in width midlenght, with two subdistal and three long simple distal setae.

Mouthparts (Figure 31E, F): labrum (Figure 31E) prominent, naked. Mandibles absent. Maxillule not recovered and probably absent. Maxilliped (Figure 31F) remarkably well-developed for a non-feeding male; basis with one long lateral seta; endites with three spiniform setae on distal margin and one long outer, one shorter and three tiny setae on inner distal margin. Palp article 1 naked; article 2 with three inner, simple and one outer setae; article 3 with five longer simple inner setae; article 4 with five simple setae. Epignath not recovered.

Cheliped (Figure 32A): not elongated, attached to body via triangular sclerite. Basis widest distally, shorter than carpus, naked. Merus triangular, with one ventral seta. Carpus shorter than propodus including fixed finger, with one dorsoproximal and dorsodistal seta, and two ventromedial setae. Propodus with one seta at dactylus insertion and vertical row of 13 inner distal setae increasing in length ventrally. Fixed finger with small denticles and three simple setae on cutting edge, and two ventral setae. Dactylus as long as fixed finger, with dorsoproximal setae and setules, with three inner minute spines.

Pereopod 1 (Figure 32B) thin and sticky-like. Coxa with seta. Basis slender (l/w ratio 7.5) and naked. Ischium with one simple ventral seta. Merus about 0.8 times as long as carpus, with one robust ventral seta. Carpus longer than propodus, with two long and one short spiniform distal setae. Propodus about 0.4 times as long as basis, ventral margin with small evenly-spaced minute spines, with four distal setae, and one sub-ventrodistal spiniform seta. Dactylus and unguis marginally shorter than propodus, dactylus marginally longer than unguis, with proximal dorsal spine. Unguis with bifurcated apex.

Pereopod 2 (Figure 32C): similar to pereopod 1 except: carpus with additional simple seta, not longer than propodus. Propodus with one dorso-subdistal and one spiniform ventral setae subdistally.

Pereopod 3 (Figure 32D): similar to pereopod 2 except: propodus with two dorso-subdistal setae.

Pereopods 4 and 5 (Figure 32E, F): coxa incompletely fused to body. Basis wider than those of pereopods 1–3, naked. Ischium with two simple setae. Merus with two dissimilar spiniform distal setae. Carpus with one ‘bone-shaped’ dorsodistal seta and four spiniform distal setae. Propodus with one dorsomedial setulate, one dorsodistal, and two spiniform ventro-subdistal setae, and small dorsodistal spine. Dactylus and unguis combined shorter than propodus, without ventral spines, unguis less than half as long as dactylus.

Pereopod 6 (Figure 32G): as pereopod 5 except: propodus medial margin with spines, dorsal margin serrated, with three dorsodistal and two ventral spiniform setae and no dorsomedial seta.

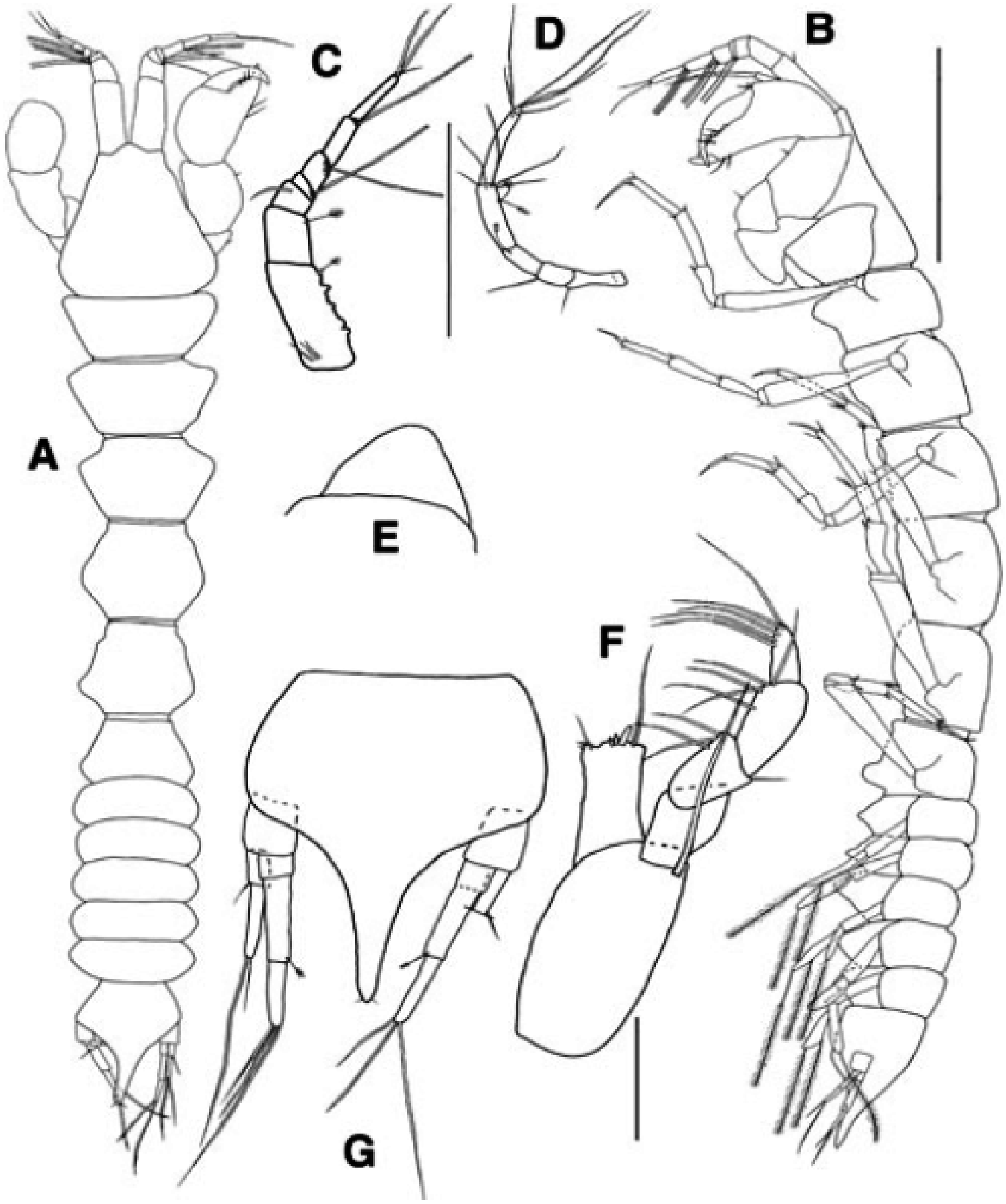


Figure 31. *Cheliasetosatanais spinimaxillipedus* n. sp., adult male paratype: (A) dorsal view; (B) same lateral view; (C) antennule; (D) antenna; (E) labrum dorsal view; (F) maxilliped; (G) pleotelson and uropod. Scale bars: A, B, 1 mm; (C, D, H), 0.5 mm; (E–G), 0.1 mm.

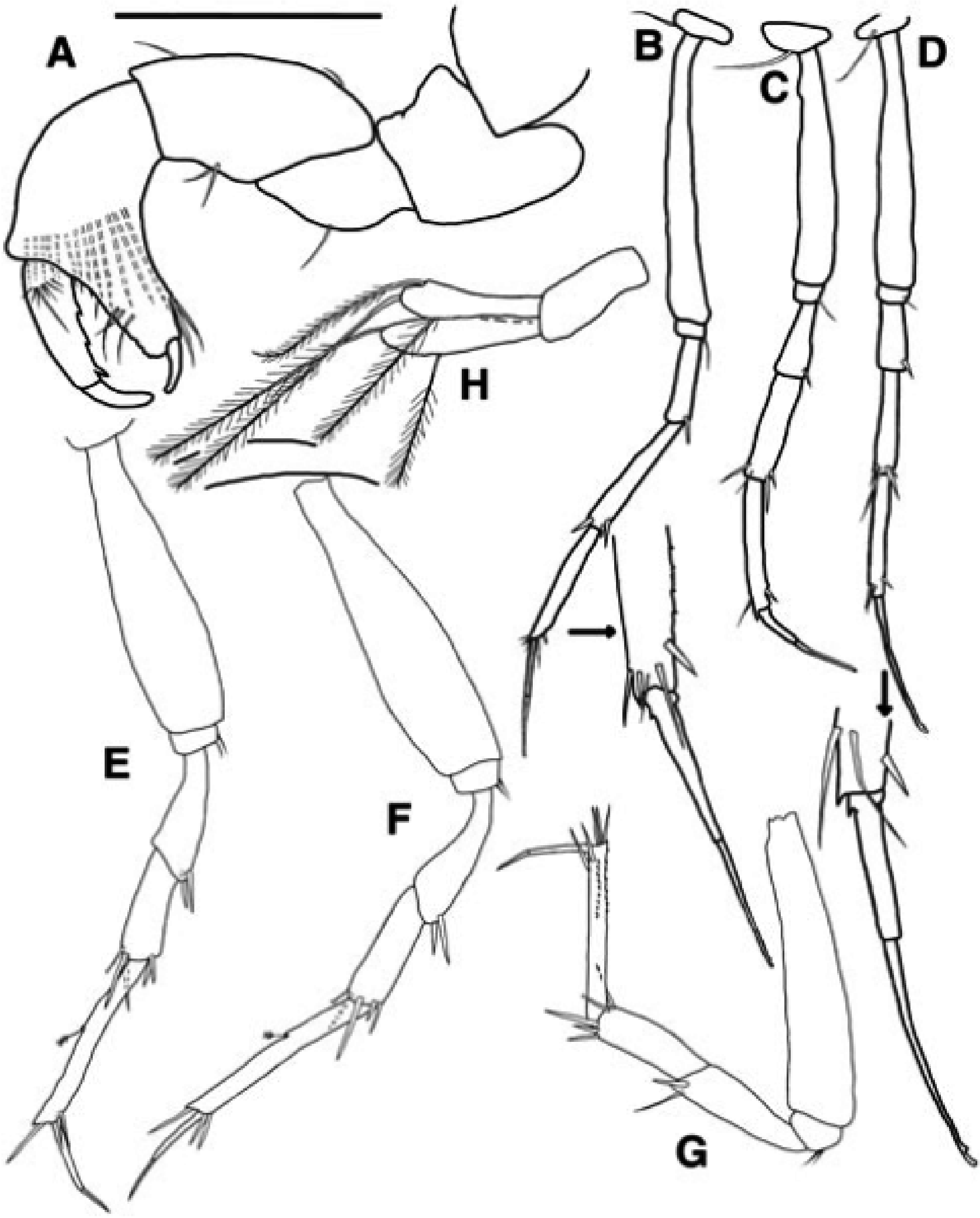


Figure 32. *Cheliasetosatanais spinimaxillipedus* n. sp., male paratype: (A) cheliped, outer view; (B) pereopod 1; (C) pereopod 2; (D) pereopod 3; (E) pereopod 4; (F) pereopod 5; (G) pereopod 6; (H) pleopod. Scale bar: (A–G), 0.5 mm.

Pleopods (Figure 32H) subequal. Basal article as long as endopod, naked. Endopod with one outer and nine plumose inner setae of which the most distal is shorter and have a complex tip. Exopod with 13 plumose inner setae (only flanking setae illustrated).

Uropod (Figure 31G): shorter than pleotelson. Basal article shorter than exopod, naked. Endopod with three articles of which the first is naked, partly fused with, and shorter than half of article 2. Article 2 longer than article 3, with one setulate distal seta. Article 3 as long as exopod article 2, with three apical setae. Exopod with two articles, as long as two first endopod articles combined; article 1 with one distal simple seta; article 2 with one short and one longer than endopod distal setae.

Acknowledgements

Thanks are extended to Drs Menot (IFREMER) and Rühlemann (BGR), chief scientists of the BIONOD expedition for inviting the senior author to participate in this cruise and for making the material available for study.

Financial support

K.L. was supported by the European Regional Development Fund (ERDF) through the COMPETE—Operational Competitiveness Program and national funds through FCT—Foundation for Science and Technology, under the project PEst-C/MAR/LA0015/2013. This paper is part of a Ph.D dissertation (C.L.A.S.) funded by CAPES—Coordenacão de Aperfeiçoamento de Pessoal de Nível Superior (Grant number: 5428/10-6).

References

Bird, G. & Holdich, D.M. (1984). New deep-sea leptognatid tanaids (Crustacea, Tanaidacea) from the north-east Atlantic. *Zoologica Scripta,* 13: 285–315.

Bird, G. & Larsen, K. (2009). Tanaidacean phylogeny: the second step. The basal Paratanaoidean families. *Arthropod Systematics and Phylogeny*, 67: 137–158.

Dana, J.D. (1849). Conspectus Crustaceorum, conspectus of the Crustacea of the US Exploring Expedition. *American Journal of Science,* 2: 424–428.

Guerrero-Kommritz, J. & Brandt, A. (2005). Phylogenetic analysis of genera of 'Akanthophoreinae' (Crustacea: Tanaidacea). *Organisms, Diversity and Evolution,* 5: 285–296.

Hansen, H.J. (1913). Crustacea, Malacostraca. II. IV. *The Order Tanaidacea*. Danish Ingolf Expedition, 3: 1–145.

Kakui, K., Katoh, T., Hiruta, S.F., Kobayashi, N. & Kajihara H. (2011). Molecular systematics of Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of suborder/superfamily-level Classification. *Zoological Science,* 28: 749–757.

Knight, J., Larsen, K. & Heard, R. (2003). Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico, XIII: a new deep-sea tanaidomorphan genus. *Proceedings of the Biological Society of Washington,* 116: 497–502.

Kudinova-Pasternak, R.K. (1983). The abyssal Tanaidacea (Crustacea) of Iberian and West-European hollows of the Atlantic Ocean. *Zoologicheskii Zhurnal,* 62: 1170–1176.

Lang, K. (1949). Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologie,* 42: 1–14.

Lang, K. (1971). Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen, 6. Revision der Gattung *Paranarthrura* Hansen, 1913 und Aufstellung von zwei neuen Familien, vier neuen Gattungen und zwei neuen Arten. *Arkiv för Zoologi,* 23: 361–401.

Lang, K. (1972). *Siphonolabrum mirabile* n. gen., sp. nov. (Tanaidacea). *Crustaceana* 3 (Supplement), 214–220.

Larsen, K. (1999). Pacific Tanaidacea (Crustacea); the genus *Agathotanais*, with descriptions of three new species. *Records of the Australian Museum,* 51: 99–112.

Larsen, K. (2000). Revision of the genus *Collettea* (Crustacea: Tanaidacea). *Invertebrate Taxonomy,* 14: 681–693.

Larsen, K. (2001). Morphological and molecular investigation of polymorphism and cryptic species in tanaid crustaceans: implications for tanaid systematics and biodiversity estimates. *Zoological Journal of the Linnean Society,* 131: 353–379.

Larsen, K. (2002). Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico, X: the question of being male. *Gulf and Caribbean Research,* 14: 53–66.

Larsen, K. (2003). Proposed new standardized anatomical terminology for Tanaidacea (Peracarida). *Journal of Crustacean Biology,* 23: 644–661.

Larsen, K. (2005). *Deep-sea Tanaidacea (Peracarida) from the Gulf of Mexico*. Crustaceana Monographs 5. Leiden: Brill, 387 pp.

Larsen, K. (2011a). Tanaidaceans from the Central Pacific Manganese Nodule Province. I. The genera *Collettea*, *Robustochelia* and *Tumidochelia*. *ZooKeys,* 87: 19–41.

Larsen, K. (2011b). Tanaidacean assemblage from the Central Pacific Manganese Nodule Province. II. The genera *Stenotanais* and *Typhlotanais*. *Zootaxa,* 3088: 39–53.

Larsen, K. & Froufe, E. (2010). Identification of polymorphic species within groups of morphologically conservative taxa: combining morphological and molecular techniques. In Nimis P.L. and Vignes-Lebbe R. (eds.), *Tools for identifying biodiversity: progress and problems*. Trieste: Edizioni Universita` di Trieste, pp. 301–305.

Larsen, K. & Froufe, E. (2013). A new polymorphic species of *Leptochelia* (Crustacea: Tanaidacea) from Guinea Bissau, West Africa, with comments of genetic variation within *Leptochelia*. *African Invertebrates,* 54: 105–125.

Larsen, K., Bird, G. & Ota, M. (2013). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited I: the family Agathotanaidae Lang, with description of four new species. *Zootaxa,* 3630: 424–444.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny. The first step: the superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research,* 40: 205–222.

Sars, G.O. (1882). Revision af Gruppen: Isopoda Chelifera med Characteristik af nye herhen hørende Arter og Slægter. *Archiv for Matematik og Naturvidenskab,* 7: 1–54.

Sieg, J. (1976). Zum natu¨rlichen System der Dikonophora Lang (Crustacea, Tanaidacea). *Zeitschrift fu¨r Zoologische Systematik und Evolutionsforschung,* 14: 177–198.

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzieger,* 205: 401–416.

Sieg, J. (1986). Crustacea Tanaidacea of the Antarctic and Subantarctic. 1. On material collected at Tierra del Fuego, Isla de los Estados and the west coast of the Antarctic peninsula. *Biology of the Antarctic Seas,* 45: 1–180.

doi:10.1017/S0025315414000101

Zootaxa, 4018 (4): 535–552 (2015)

Article 5. Two new species of family Neotanaidae (Peracarida: Tanaidacea) from the Antarctic and Mid-Pacific Oceans.

Catarina L. Araújo-Silva[1,2,4], Elsa Froufe[1] & Kim Larsen[3]

[1]CIIMAR (Interdisciplinary Centre of Marine and Environmental Research), AEE (Laboratory of Aquatic Ecology and Evolution), Porto University, Rua dos Bragas, 289, 4050-123 Porto, Portugal. [2]Capes Foundation, Ministry of Education of Brazil, Brasília–DF, 70040–020 Brazil. [3]ENSPAC Department of Environmental, Social and Spatial Change, 11.2, Roskilde University Center. DK-4000 Roskilde, Denmark. [4]Corresponding author (E-mail: katelas@hotmail.com)

Abstract

Samples collected from the Antarctic (ANDEEP/2002) and Mid-Pacific (BIONOD/2012) Oceans allowed analyses of several specimens of the family Neotanaidae. From these surveys two new species are described: *Neotanais bicornutus* and *Venusticrus thor*. The new material led to a re-diagnosis of *Venusticrus*, and *N. rotermundiae* is now assigned to this genus. The male of *N. bicornutus* shares a number of characters with the "robustus" species group, but differs by having a pleotelson about 1.5 times as wide as long, cheliped carpus about 1.5 times as long as cephalothorax, cheliped propodus with two long dorsal projections, and uropod endopod article 1 with 8–10 fine setae proximal to mid-length on outer margin. The *N. bicornutus* preparatory female differs from all species by a combination of characters including the number of setae on dorsal margin of cheliped carpus (about 15 setae), the uropod attachment slightly posterior to mid-length, uropod basal article about 2.7 times as long as endopod article 1. The female of *V. thor* differs from those of *V. insolitus*, *V. glandurus* and *V. rotermundiae* by the body proportions, the pleon having three lateral setae on epimera, pleon with a blunt ventral keel, pereopodal setation, number of setae on maxilliped endite and basis as well as other characters. Total genomic DNA was extracted from two specimens of *V. thor* and sequences of two genes, i.e., cytochrome oxidase 1 (COI) and ribosomal (28S) were obtained.

Key words: *Neotanais, Venusticrus*, COI, 28S, ANDEEP, Antarctic, Mid-Pacific

Introduction

The superfamily Neotanaoidea Sieg, 1980 consists of one family, Neotanaidae Lang, 1956 and is considered one of the largest tanaidacean families, comprised of 51 (with two described herein) species (Anderson 2013; Wi *et al*. 2014, 2015). This family is restricted to deep water and currently holds four genera (*Carololangia* Gardiner, 1975; *Herpotanais* Wolff, 1956a; *Neotanais* Beddard, 1886; *Venusticrus* Gardiner, 1975). Neotanaids are geographically widespread with 24 species originally described from the Pacific and two, four and 19 from the Indian, Antarctic and Atlantic oceans, respectively. Despite the distributional separation, the morphology of the females is highly conservative while the males are polymorphic. This might suggest gene flow or genetic lag between populations (Gardiner 1975) which potentially could be attributed to the higher mobility of this taxon relative to Tanaidomorpha (Larsen 2005).

Before the type genus *Neotanais* was elevated to the family rank by Lang (1956), the genus was first included within the Tanaididae (Beddard, 1886) and later Paratanaidae (Lang, 1949). Afterwards, Sieg (1980) created the suborders Apseudomorpha, Neotanaidomorpha and Tanaidomorpha; he considered Neotanaidomorpha had too many shared characters with both Apseudomorpha and Tanaidomorpha to be placed within either and elevated the taxon to suborder rank.

Recently, Kakui *et al*. (2011) presented a phylogenetic study of the Tanaidacea based on a molecular analysis. Their results showed that the suborder Neotanaidomorpha nested within Tanaidomorpha, with strong support, and it was reduced to superfamily rank. This result conflicts with previous phylogenies based on morphological characters (Larsen & Wilson 2002). Also the general life-style between neotanaids and tanaidomorphans differs considerably e.g., neotanaids are free-living surface dwellers (Gardiner 1975; Thistle *et al.* 1985) while tanaidomorphans are mostly, if not exclusively, tube dwellers (Johnson & Attramadal 1982a, b; Mendoza 1982; Holdich & Jones 1983).

This study aims to analyse morphologically several neotanaid specimens and describe one new species of *Neotanais* collected in the Antarctic

(ANDEEP/2002) and one of *Venusticrus*, sampled from Manganese Nodules-Pacific Ocean (BIONOD/2012). In addition, mtDNA COI and r28S genes were sequenced from two *Venusticrus* specimens and submitted to GenBank.

Material and Methods

Taxonomy

The specimens of *Neotanais bicornutus* n. sp. (see below) were collected from the survey ANDEEP/2002 (Antarctic) and *Venusticrus thor* n. sp. (see below) from BIONOD/2012 (Mid-Pacific) (for information on that material see Larsen & Araújo-Silva (2014a, b)).

Terminology follows Larsen (2003). Dissections were made with chemically sharpened tungsten wire needles and then placed on slides with glycerin and chlorazol black, covered by a cover slip and sealed with nail polish. Habitus illustrations were made from holotypes and allotypes while appendages were dissected and drawn from paratypes via a camera lucida attached to an Olympus compound microscope. Drawings were made with the aid of the computer program CorelDraw. Type material of *N. bicornutus* is kept at the Natural History Museum, Hamburg, Germany (DZMB ZMH) while *V. thor* at the Muséum National d'Histoire Naturelle Paris, France (MNHN).

Molecular

Total genomic DNA was extracted from two specimens of *V. thor* and sequences of two genes, i.e., cytochrome *c* oxidase subunit 1 (COI) and 28S ribosomal RNA (28S) were obtained. Primers used, PCR reactions, and sequencing conditions for both genes are described in Larsen *et al.* (2014), except for the DNA template volumes that were 1.0 µL. The cycle parameters are as follow: initial denaturation at 94°C (3 min), denaturation at 94°C (30 s), annealing temperature at 45°C (COI) and 46ºC (28S) both for 1 min and extension at 72°C (1 min 30s) repeated for 44 cycles, with a final extension of 10 min at 72°C. Sequences were read on an ABI-310 and are available on GenBank (accession numbers: 28S - KT592230, KT592231; COI - KT592232, KT592233).

Systematics

Order Tanaidacea Dana, 1849

Suborder Tanaidomorpha Sieg, 1980

Superfamily Neotanaoidea Sieg, 1980

Family Neotanaidae Lang, 1956

Genus *Neotanais* Beddard, 1886

Diagnosis. For females, see Weigmann & Guerrero-Kommritz (2009: 21).

Gender. Masculine

Type-species. *Neotanais americanus* Beddard, 1886

Generic remarks. According to Larsen (2005) and Bamber (2007) the following combination of characters have been useful to distinguish the species (females): relative length/width (l/w) of cephalothorax, pereonites, pleotelson, cheliped propodus, antennae, and uropods; the shape of pleonal ventral keel; number of cheliped dorsal carpal setae; the l/w of the cheliped fixed finger and dactylus; proportions of article 1 and relative lengths of the distal articles of the antennule; relative length of the uropod exopod with the first article of the uropod endopod and the adult size.

Neotanais bicornutus **n. sp.**

(Figures 33–35)

Material examined. Holotype: female with oostegites (ZMHK 45086), body total length: 9.7 mm, ANT XIX-3 ANDEEP I Sta. 42-2/EBS-SUPRA, 59º 24’ 10’’ S, 57º 21’ 15’’ W, 27 January 2002, depth 3683 m.

Allotype: copulatory male (damaged, partly dissected—ZMHK 45088), body total length: 20.6 mm, ANDEEP II Sta. 140-8/EBS-Supra, 58° 9’ 35’’ S, 24° 32’ 14’’ W, 22 March 2002, depth 2947 m.

Paratype: one female without oostegites, body total length: 5.21 mm (dissected, body partially preserved - ZMHK 45087), same locality of allotype.

Etymology. The name reflects the presence of two projections found on the dorsal male chelipedal propodus, similar to a "cornus”, i.e. horn, in Latin.

Diagnosis. **Female**, with oostegites: body six times as long as wide. Cephalothorax marginally longer than first two pereonites combined, no apparent rostrum or setae. Pereonites rectangular, without setae. Pleonites narrower than pereon and pleotelson, pleon lateral epimera with three plumose setae, mid-ventral keel very weekly pronounced. Pleotelson 0.6 times as long as wide, no setation. Antennule as long as cephalothorax, article 1 about 3.3 times as long as wide. Maxilliped basis broad, without proximal seta, endite with three spiniform and one bipinnate inner distal setae. Cheliped carpus with two simple ventral setae and about 15 simple dorsal setae. Uropod attachment slightly posterior to mid-length, basal article about 2.7 times as long as article 1 of endopod, exopod biarticulate, marginally shorter than endopod article 1. **Male**, copulatory male: larger than female, about 7.2 times as long as wide. Body with no apparent setae. Cephalothorax about 1.5 times as long as the first two pereonites combined. Pereonites rectangular, without setae. Pleon and pleotelson naked, uropod attached mid-length on pleotelson. Antennule 0.8 times as long as cephalothorax, article 1 about 7.5 times as long as wide. Maxilliped basis robust, naked. Endite naked. Palp of four slender articles with one simple seta on article 3 and four simple distal setae on article 4. Cheliped sclerite, basis, ischium and merus naked; carpus about 1.5 times as long as cephalothorax, widening distally with one large ventral protuberance bearing one strong spine; propodus with two long dorsal projections; fixed finger with an innermedial deep groove and a tooth distally. Uropod endopod article 1 with 8–10 fine setae proximal to mid-length on outer margin.

Description. Female. Body based on female holotype and appendages from dissected paratype.

Body (Figure 33A, B): heavily calcified, dorsoventrally flattened, about six times as long as wide. Cephalothorax: about 1.2 times as long as wide and 1.1 times as long as the first two pereonites combined, no apparent rostrum or setae. Pereon: about 4.1 times as long as wide, 60% of total body length, no dorsal relief. All pereonites rectangular, no plumose or simple setae; pereonite 1 shortest, 0.4 times as long as wide; pereonites 2–6 subequal: 0.7, 0.76, 0.81, 0.87, 0.68 times as long as wide, respectively. Pleon: about 1.8 times as long as wide, 20% of total body length; all pleonites subequal, narrower than pereon and slightly narrower than pleotelson, lateral epimera with about three plumose setae, mid-ventral keel very weekly pronounced (Figure 33D). Pleotelson 0.6 times as long as wide, no apparent setation; uropod attachment slightly posterior to mid-length.

Antennule (Figure 34A): as long as cephalothorax. Article 1 longest, about 3.3 times as long as wide, with one setulose and four simple distal setae. Article 2 about three times shorter than article 1, with four simple distal setae. Article 3 about 1.2 times as long as wide, 1.6 times shorter than previous article, with two simple distal setae. Article 4 1.2 times as long as article 3 and three times as long as wide, naked. Articles 5–7 marginally shorter than article 4, with one simple and one annulated aesthetasc on article 5; article 6 with one annulated aesthetasc; article 7 with three simple distal setae.

Antenna (Figure 34B): marginally shorter than antennule (0.8 times). Article 1 broader than others articles, about 1.6 times as long as wide and, as long as articles 3 and 4 combined, naked. Article 2 slender than article 1, about 2.6 times as long as wide, with two simple distal setae. Article 3 as long as wide and, as long as articles 7–8 combined, 0.4 times as short as article 2, with one simple distal seta. Article 4 about two times as long as wide, naked. Article 5 marginally longer than article 2, about 3.3 times as long as wide, with two simple distal setae. Article 6 about 1.2 times as long as article 3, naked. Articles 7 and 8 both short, with three and five simple distal setae, respectively.

Mouthparts (Figure 34C–J): labrum (Figure 34C) subtriangular, with several fine setules at the tip, anterior lateral margins depressed. Mandibles (Figure 34D, E) molar with several distal pointed denticles. Left mandible (Figure 34D) incisor longer than *lacinia mobilis*, with several blunt denticles, setal row with two spiniform- serrated setae; lacinia mobilis well developed with four crenulated denticles. Right mandible (Figure 34E) incisor with several blunt crenulated denticles, setal row with four spiniform- serrated setae. Labium (Figure 34H) palp elongated with several setules at tip and two small spiniform setae, lobes with distal and lateral rows of setules. Maxillule (Figure 34F, G) outer endite (Figure 34F) with eight spiniform distal setae as well as several fine lateral setae; inner endite (Figure 34G) one long and two short bipinnate setae and one short spiniform seta. Maxilla (Figure 34I) inner lobe of fixed endite with several distal setae; outer lobe with two spiniform setae; inner lobe of movable endite with three spiniform setae, outer lobe with two spiniform and three bifurcate spiniform setae.

Maxilliped (Figure 34J) endite with three inner distal spiniform setae, one bipinnate spiniform and several fine setae along the distal margin. Basis broad, palp pedestal (see Larsen 2005: 11) with one long simple distal seta. Palp article 1 naked, as long as article 3; article 2 shortest, with one outer distal simple seta and six inner simple setae; article 3 about 1.4 times as long as article 2, with eight simple inner setae; article 4 slender and longest than the other articles, four times as long as wide, with three pinnate and four simple setae. Epignath not recovered.

Cheliped (Figure 33C): sclerite rectangular (illustrated on Figure 33B). Basis tapering distally, about 1.1 times as long as wide, naked. Ischium very short, hardly visible. Merus with one simple seta. Carpus about 1.1 times as long as basis, about twice as long as wide; with two simple ventral setae and, 15 simple setae along dorsal margin. Propodus slightly shorter than basis, no setae. Fixed finger with one simple inner proximal seta, three distal and two on outer margin next to unguis; dactylus shorter than fixed finger with two short spines in the inner margin.

Pereopod 1 (Figure 35A): coxa small, naked. Basis slender, about 4.1 times as long as wide, slightly longer than the three next articles combined, with four dorsoproximal and two plumose ventral setae. Ischium with two simple setae. Merus about 1.5 times as long as carpus, with two bipinnate medial setae. Carpus shortest, about 1.7 times as long as wide, with three simple medial setae, one spiniform- serrated distal and, three long- bipinnate distal setae. Propodus as long as dactylus and unguis combined, about 2.9 times as long as wide, with one setulose medial, two simple distal, one spiniform- serrated hook-like, and four spiniform- bipinnate setae. Dactylus and unguis thin, naked.

Pereopod 2 (Figure 35B): articles with similar length and armament as pereopod 1 except: basis with two ventral and one setulose dorsal setae. Carpus about 0.8 times as long as merus, with four simple medial setae. Propodus with seven spiniform- bipinnate ventral setae. Dactylus with one fine simple proximal seta; unguis broken.

Pereopod 3 (Figure 35C): articles with similar length to pereopod 2 except: coxa with one simple seta. Basis about three times as long as wide, with two dorsal and one ventral setulose setae. Carpus about 1.2 times as long as merus, with three simple medial and four bipinnate ventral setae. Propodus with three simple distal setae.

Pereopod 4 (Figure 35D): coxa absent. Basis about 4.2 times as long as wide, with one dorsoproximal and three setulose ventral setae. Ischium with three simple setae. Merus shortest, about 0.8 times as long as carpus, with three bipinnate distal setae. Carpus marginally shorter than propodus, with six bipinnate and one small simple distal setae. Propodus as long as dactylus and unguis combined (without the terminal seta), with five spiniform bipinnate, three simple and one setulose setae. Dactylus with denticles arranged in a ring around the insertion of unguis; unguis slender with two ventral rows of small spines.

Pereopod 5 (Figure 35E): articles with similar length to pereopod 4 except: basis with two setulose ventral setae.

Pereopod 6 (Figure 35F): articles with similar length to pereopod 5 except: basis with one setulose dorsoproximal seta. Ischium with two simple setae. Merus with two bipinnate distal setae. Carpus with five bipinnate distal and three simple setae. Propodus with seven bipinnate, two simple and about five spiniform serrated setae next to dactylus insertion.

Pleopods (Figure 33E): basal article about 1.6 times as long as wide, with three plumose setae. Exopod with 13 plumose setae. Endopod with three inner and eleven outer plumose setae.

Uropod (Figure 34K): basal article naked, about 2.7 times as long as article 1. Endopod (damaged) with five articles. Articles 1–4 bearing one to four simple setae, except article 4, naked. Article 5 longer, bearing five simple distal setae. Exopod biarticulate, marginally shorter than article 1 of endopod, with one simple seta each article.

Description. Copulatory male allotype.

Body (Figure 33F): heavily calcified, no apparent setae. Dorsoventrally flattened, about 7.2 times as long as wide. Cephalothorax: about 1.4 times as long as wide and 1.5 times as long as the first two pereonites combined, with visible rostrum, with two strong anterolateral spines. Pereon: about 3.7 times as long as wide, about 50% of total body length. All pereonites rectangular, no plumose or simple setae; pereonite 1 shortest, 0.3 times as long as wide; pereonites 2 and 3 subequal, 0.5 and 0.7, respectively; pereonites 4 and 5 similar; pereonite 6 about 0.6 times as long as wide. Pleon: no mid-ventral spur (Figure 33G); about 1.6 times as long as wide, 30% of total body length; all pleonites subequal, as wide as cephalothorax and pereonite 1, lateral epimera with no seta. Pleotelson (Figure 33I) about 0.6 times as long as wide, no apparent seta; uropod attachment mid-length on pleotelson.

Antennule (Figure 34L): damaged. Article 1 longest, 0.8 times as long as cephalothorax, about 7.5 times as long as wide, with five proximal and six simple subdistal setae. Article 2 about 2.1 times as long as wide, twice as long as articles 3 and 4 combined, with five simple medial setae. Article 3 naked. Article 4 short bearing several aesthetascs. Other articles missed.

Mouthparts and maxilliped (Figure 34M): all reduced, except: maxilliped basis robust, longer than wide, naked. Endite naked. Palp article 1 naked, short; article 2 about 2.2 times as long as article 1, naked; article 3 about 1.3 times as long as article 2, with one simple proximal seta; article 4 longest, about 1.2 times as long as article 3, with four simple distal setae.

Cheliped (Figure 33H): sclerite (not illustrated), naked. Basis short, naked. Ischium shaped as a narrow incomplete band extending from under the merus. Merus short, naked. Carpus 1.5 times as long as cephalothorax, widening distally, with one simple seta and one visible protuberance bearing one long strong spine on ventral side. Propodus with two strong dorsal projections and a third less visible (next to dactylus insertion), with slight crenation and one simple seta next to dactylus insertion. Fixed finger inner margin with one simple seta, one deep groove medial and one tooth distally. Dactylus marginally longer than fixed finger, with three proximal denticles and a row of denticles distally.

Uropod (Figure 33I): basal article attached at mid-lateral margin, about 1.2 times as long as article 1 of endopod. Endopod damaged, article 1 with 8–10 fine setae proximal to mid-length on outer margin. Exopod biarticulate, half size of endopod article 1, with one simple seta on each article.

Pleopods (not illustrated): basal article apparently naked. Exopod with two apparent articles (at least a fusion line), first article bearing three and

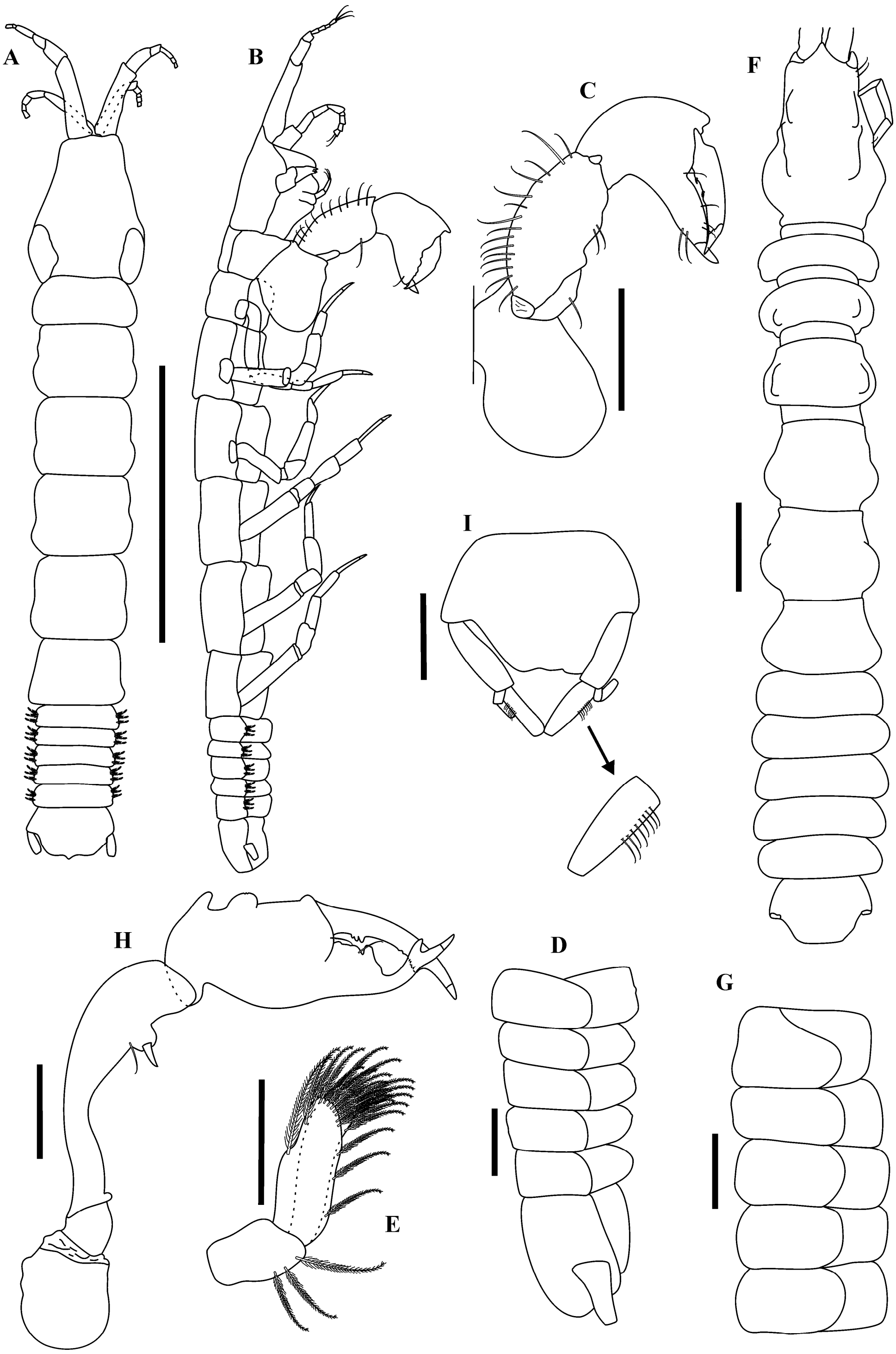


Figure 33. *Neotanais bicornutus* n. sp., female with oostegites (ZMHK 45086): (A), holotype habitus dorsal view; (B), holotype habitus lateral view. Female paratype (ZMHK 45087): (C), cheliped; (D), pleon and pleotelson; (E), pleopod. Copulatory male allotype (ZMHK 45088): (F), habitus dorsal view; (G), pleon; (H), cheliped; (I), pleotelson and uropod. Scale bars: (A, B, F, H) = 2 mm; (C) = 0.5 mm; (D, E) = 0.2 mm; (G, I) = 1 mm.

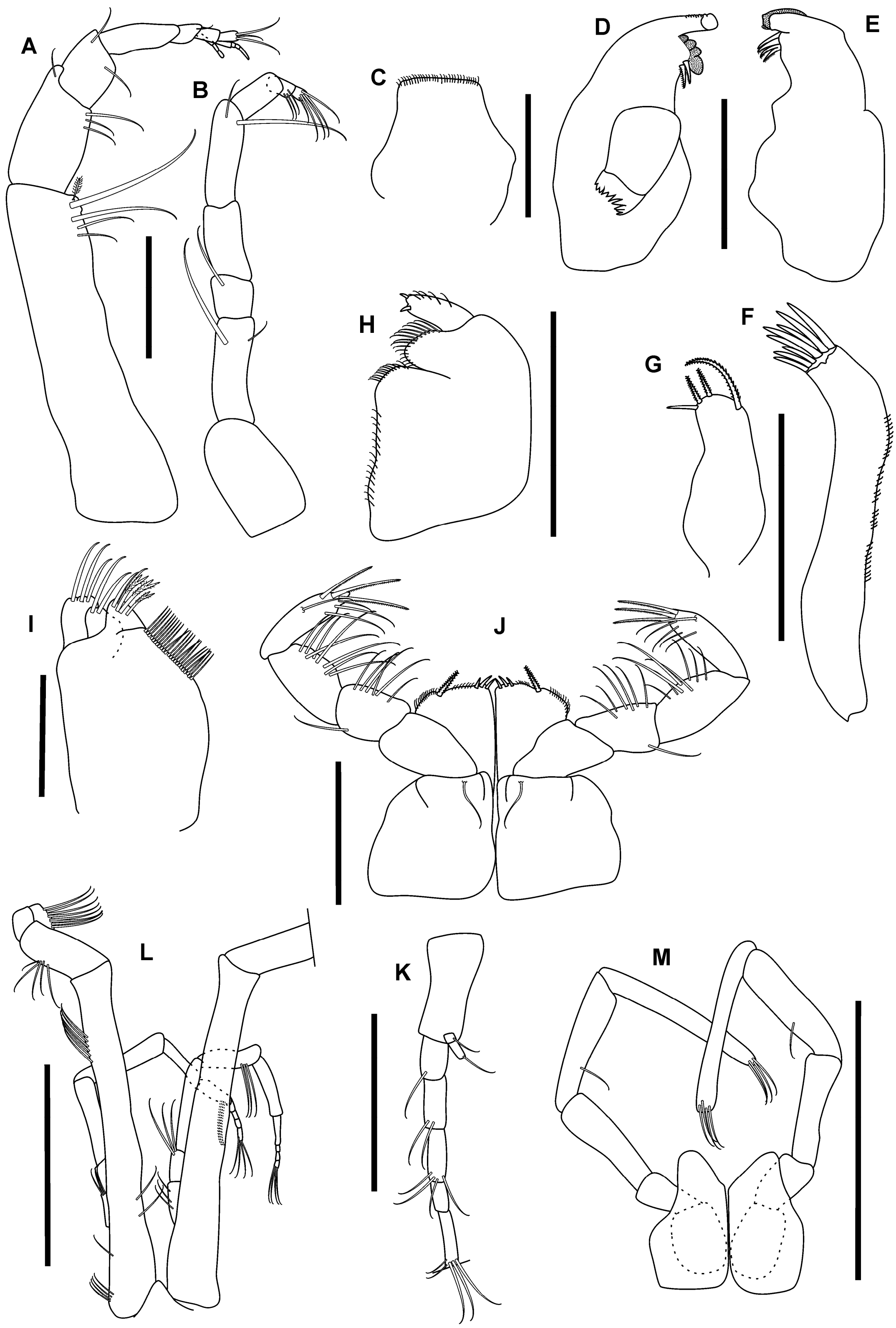


Figure 34. *Neotanais bicornutus* n. sp., female paratype: (A), antennule; (B), antenna; (C), labrum; (D), left mandible; (E), right mandible; (F), maxillule, outer endite; (G), maxillule, inner endite; (H), labium; (I), maxilla; (J), maxilliped; (K), uropod; copulatory male allotype: (L), antennule and antenna; (M), maxilliped. Scale bars: (A–J) = 0.2 mm; (K) = 0.5 mm; (L, M) = 2 mm.

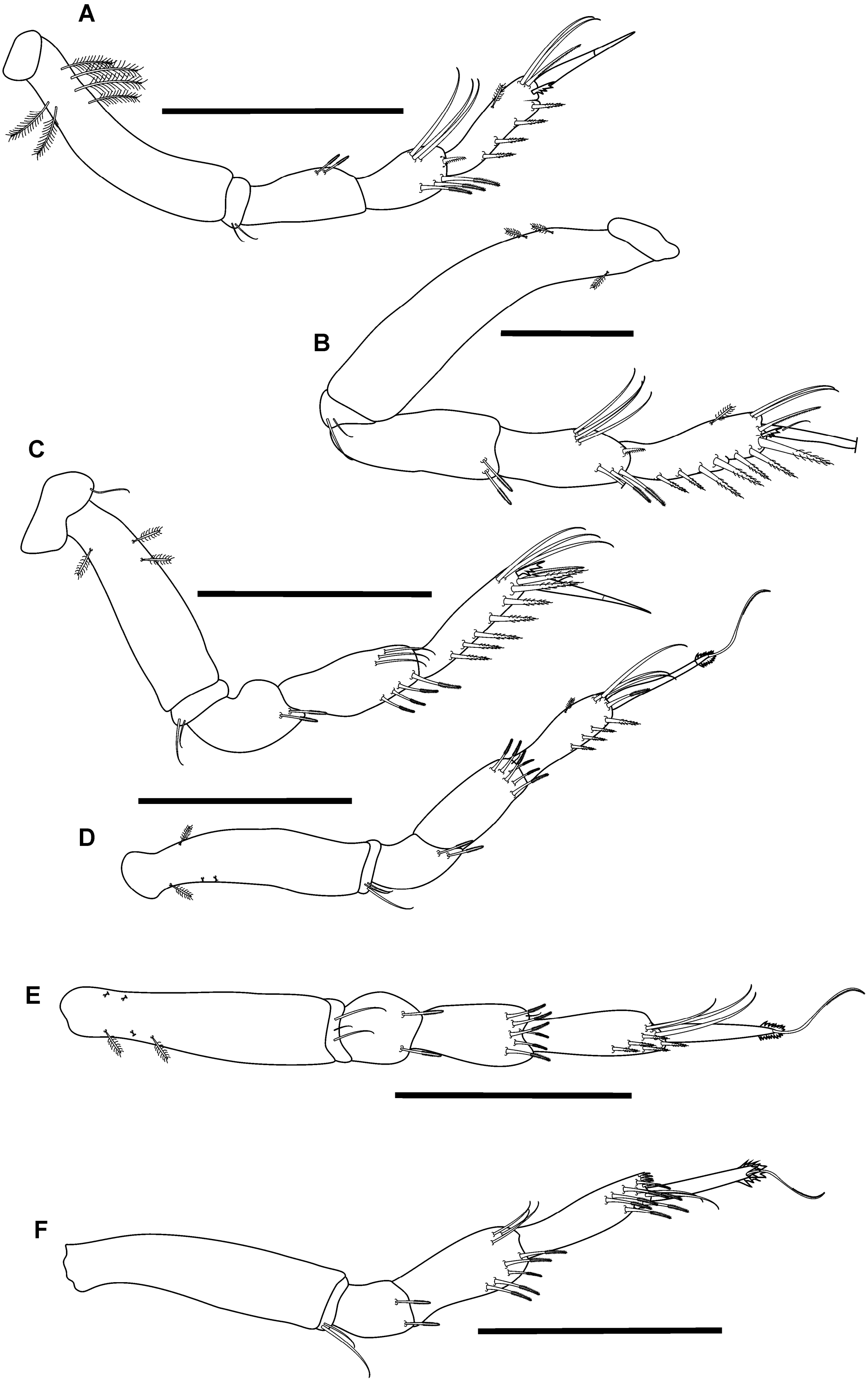


Figure 35. *Neotanais bicornutus* n. sp., female paratype: (A), pereopod 1; (B), pereopod 2; (C), pereopod 3; (D), pereopod 4; (E), pereopod 5; (F), pereopod 6. Scale bars: (A, C–F) = 0.5 mm; (B) = 0.2 mm.

second with about 25–30 plumose setae. Endopod with about 30 inner and three plumose outer setae.

Remarks. The specimens of *Neotanais bicornutus* n. sp. were collected in the Antarctic Ocean and when compared to Gardiner's (1975) *Neotanais* scheme, it mostly resembles with the "robustus" group, which hitherto held *N. robustus* Wolff, 1956b, *N. antarcticus* Kussakin, 1967 and *N. tuberculatus* Kudinova-Pasternak, 1970. Gardiner (1975) recognized this group based mainly on copulatory male characters, although identification of neotanaid males to species is difficult owing to their strong sexual polymorphism (Larsen & Błażewicz-Paszkowycz 2003; Larsen 2005). Males are also frequently larger than females and show sexual dimorphism in the proportions of the cephalothorax and the shape of the cheliped (Bamber 2007).

The male of *N. bicornutus* shares many characters with the "robustus" group by having a pleotelson about 1.5 times as wide as long (1.4 times in *N. robustus*, 1.7 in *N. antarcticus*), the pleonites are broad and rounded laterally in dorsal view, lateral epimera without apparent seta, and they also bear a strong ventral spine arising from a protuberance on the cheliped carpus (Figure 33H). However, *N. bicornutus* differs from the "robustus" group by having a dorsally naked cheliped carpus (while there are four setae in *N. tuberculatus*, five in *N. antarcticus* and apparently two or three tiny setae in *N. robustus*). The uropod endopod article 1 has 8–10 fine setae proximal to mid-length on outer margin, while these setae are lacking in the "robustus" group, but are found in *N. hadalis* Wolff, 1956a and *N. mesostenoceps* Gardiner, 1975. It further differs in having a cheliped propodus with two strong and long dorsal projections; within the "robustus" group only in *N. robustus* are there propodus projections, one small dorsal and one longer ventral. The propodal dorsal crest is very slight in *N. bicornutus*, while in other species this character is rather pronounced.

The females vary mainly in the number of setae on the dorsal margin of the cheliped carpus; *N. bicornutus* has about 15 setae, while there are nine in *N. robustus*, three in *N. antarcticus* and seven in *N. tuberculatus*. Also, the pleonal epimera have three plumose setae, while the other "robustus" group species apparently lack this feature. *Neotanais bicornutus* also resembles the Antarctic species *N. krappschickelae* Larsen & Błażewicz-Paszkowycz, 2003, in having a ring of spines on the unguis of pereopods 4–6 and the many dorsal setae on the cheliped carpus (about 24 setae in *N. krappschickelae* and 15 setae in *N. bicornutus*). However, they can be easily distinguished by the number of the plumose setae on almost all pereopod articles of both genders, the number of setae on the first antennule article (about eleven plumose [described as bipinnate] in *N. krappschickelae* while *N. bicornutus* has two simple and two plumose setae), the epimera setae (absent in *N. krappschickelae* while *N. bicornutus* has three), the body size as well as other characters.

Genus *Venusticrus* Gardiner, 1975

Generic remarks. *Neotanais rotermundiae* Weigmann & Guerrero-Kommritz, 2009 shares several characters with *V. glandurus* such as the uropod attached ventrally to the pleotelson (possibly an apomorphic character for *Venusticrus*) and the distal bilobate and finely serrated terminal shield at insertion of the unguis of pereopods 4–6 (so far found only in species of *Venusticrus*), therefore, the former is here transferred to *Venusticrus* (as *V. rotermundiae* n. comb.). In his revision of *Neotanais*, Larsen (1999) also transferred *N. insolitus* Gardiner, 1975 to *Venusticrus*, warranted by the uropod attachment, the setation on the cheliped carpus, the slim cheliped basis and ventral pereopod attachments. Nevertheless, *V. insolitus*, *V. rotermundiae* and the new species of *Venusticrus* described here, lack some of the diagnostic characters listed by Gardiner (1975). Thus, a revised generic diagnosis is presented in the present study.
Gender. Masculine
Type-species. *Venusticrus glandurus* Gardiner, 1975

Diagnosis. Female (modified after Gardiner 1975: 158). Pleonites with or without setae on lateral epimera. Pleotelson acorn-shaped, marginally wider than long. Cheliped carpus with 12–18 simple dorsal setae; propodus bearing a large, with brown-bordered dorsal crest (*V. glandurus*), or a distal margin curved and pointed (sometimes with crenulated tip). Pereopod attachments not visible in dorsal view. Pereopods 4–6 with articles bearing long plumose setae (*V. glandurus*) or with setulose, simple and bipinnate setae (all other species); dactylus with distal bilobate and finely serrated terminal shield (as described by Weigmann &

Guerrero-Kommritz (2009)); unguis slender, with two fine ventral rows of spines. Uropod basal article attached posterior to mid-length on the ventral margin of the pleotelson (not visible in dorsal view), exopod biarticulate.

Male (copulatory). Body heavily calcified, no apparent setae. Cephalothorax anterior margin relatively broad widening posteriorly. All pereonites rectangular, no seta. Pleon lateral margin rounded. Antennule article 4 bearing several long aesthetascs. Mouthparts all reduced. Cheliped sclerite, basis, ischium and merus naked, with two simple ventral setae; fixed finger reduced, in the shape of a hammer. Uropod basal article attached posterior to mid-length on the ventral margin of the pleotelson, endopod article 1 with several proximal to mid-length fine setae on outer margin.

Species included. *Venusticrus glandurus* Gardiner, 1975; *V. insolitus* (Gardiner, 1975); *V. rotermundiae* (Weigmann & Guerrero-Kommritz, 2009) comb. nov.; *V. thor* sp. nov.

Venusticrus thor **n. sp.**

(Figures 36–38)

Material examined. Holotype: female with oostegites (MNHN-IU-2014-10184), body total length: 6.6 mm, BIONOD EBS-Supra Sta. 12–51, 12º 18’ 44’’N, 118º 8’ 2’’W, 11 April 2012, depth 4274 m.

Allotype: copulatory male (MNHN-IU-2014-10185), body total length: 10.6 mm, same locality as holotype.

Paratypes: one female with oostegites (MNHN-IU-2014-10186), (dissected), body total length 7.1 mm, same locality as holotype. One female, manca II (MNHN-IU-2014-10187) body total length: 2.2 mm, same locality as holotype. Two females with oostegites (used for DNA extraction, 28S - KT592230, KT592231; COI - KT592232, KT592233), same locality as holotype. One female, manca II; one female, without oostegites (MNHN-IU-2014-10188), BIONOD EBS-Supra Sta. 12–80, 14º 3’ 23’’N, 130º 2’ 23’’W, 21 April 2012, depth 4986 m.

Etymology. The name reflects the strong shape of male cheliped dactylus and fixed finger, as if holding a hammer, like the god Thor from Nordic mythology. Noun in apposition.

Diagnosis. **Female** with oostegites. Body with pigmentation along the pereonites and pereopods, no apparent setae. Cephalothorax as long as the first two pereonites combined, with no apparent rostrum or setae. Pleonites lateral epimera with three plumose setae, ventral keel weekly pronounced. Labrum subtriangular, naked; maxilliped endite with five setulose spiniform distal setae, pedestal palp with one long distal seta, and basis with two simple proximal long setae. Cheliped carpus with about twelve simple dorsal setae; propodus with a distal margin curved and pointed crenulated at tip. Uropod attached mid-length on ventral margin, basal article about 1.8 times as long as article 1 of endopod; exopod biarticulate, half as long as endopod article 1. **Male** (copulatory): see diagnosis of *Venusticrus*.

Description. Body based on female holotype and appendages from dissected paratype.

Body (Figure 36A, B): heavily calcified, dorsoventrally flattened, about 7.9 times as long as wide, with pigmentation along the pereonites and pereopods; no apparent setae. Cephalothorax: about 1.3 times as long as wide, as long as the first two pereonites combined; no apparent rostrum or setae. Pereon: about 4.6 times as long as wide, about 57% of total body length. All pereonites rectangular; pereonite 1 shortest, about 0.5 times as long as wide; pereonite 2–5 similar. Pereonite 6 slightly short than previous pereonite, about 0.8 times as long as wide. Pleon (Figure 37K): about 2.4 times as long as wide, about 28% of total body length; all pleonites subequal, with three plumose setae on lateral epimera, ventral keel present but blunt and soft. Pleotelson (Figure 37L): rounded, marginally wider than long (1.1 times), uropod attached to mid-length on ventral margin.

Antennule (Figure 37A): marginally longer than cephalothorax. Article 1 longest, about 2.9 times as long as wide, about three times as long as article 2, with two plumose subdistal and two simple distal setae. Article 2 slightly longer than articles 3, about 1.7 times as long as wide, with two plumose and three simple distal setae. Article 3 about 1.4 times as long as wide, as long as article 4, naked. Article 4 as long as articles 5–7 combined, with three simple distal setae. Article 5 and 6 subequal with one annulated aesthetasc each. Article 7 with three simple distal setae.

Antenna (Figure 37B): about 1.5 times as long as antennule. Article 1 broader than other articles, as long as wide, as long as articles 3 and 4 combined, naked. Article 2 longest, about 3.5 times as long as wide and 3.8 times as long as article 3, with one fine spiniform distal and one plumose setae. Article 3 as long as wide, with one plumose distal seta. Article 4 about 1.8 times as long as article 3, with one plumose distal seta. Article 5 about 2.5 times as long as wide, marginally shorter than articles 6 and 7 combined, with two strong and four short simple setae, one setulose distal seta. Article 6 about 2.8 times as long article 7, with four simple distal setae. Articles 7–9 subequal, bearing three, two and four simple distal setae, respectively.

Mouthparts (Figure 37C–J): labrum (Figure 37C) subtriangular, naked. Mandibles (Figure 37D, E) heavily calcified, molar with several pointed distal denticles. Left mandible (Figure 37D) incisor with about five blunt denticles, setal row with two serrated setae; lacinia mobilis marginally longer than incisor with one or two blunt crenulated denticles. Right mandible (Figure 37E) incisor with several blunt distal denticles, setal row with two serrated setae. Labium (Figure 37H): palp elongated with several setules at tip, with two outer denticles and two inner small spiniform setae, lobes with distal and lateral setules. Maxillule (Figure 37F, G) outer endite (Figure 37F) with seven spiniform and three bipinnate distal setae; inner endite (Figure 37G) with one plumose and three short spiniform distal setae. Maxilla (Figure 37I) with several setules on ventral and lateral margins; inner lobe of fixed endite with several simple distal setae; outer lobe with two spiniform and three bifurcate spiniform setae; inner lobe of movable endite with three spiniform setae; outer lobe with two bipinnate and three spiniform setae. Maxilliped (Figure 37J) endite with five inner distal setulose spiniform setae and, several fine simple setae. Basis about 1.8 times as long as wide, with two proximal long simple setae, palp pedestal with one long simple distal seta. Palp article 1, marginally longer than article 2 (about 1.1 times), about 1.6 times as long as wide, naked; article 2 shortest, about 1.3 times as long as wide, with one simple outer distal seta and about five simple inner setae; article 3 longest, about 1.5 times as long as article 2, and about 2.2 times as long as wide, with five simple inner setae; article 4 slender, about 2.7 times as long as wide, with five pinnate and five simple setae. Epignath not recovered.

Cheliped (Figure 36C): sclerite rectangular (illustrated on Figure 36B). Basis about 1.7 times as long as wide, naked. Ischium short, hardly visible. Merus subtriangular, with one simple seta. Carpus marginally longer than basis, about 2.2 times as long as wide, with two simple ventral setae and, about 12 simple dorsal setae. Propodus slightly shorter than basis, with a distal margin curved and pointed crenulated at tip, with one simple seta at the dactylus insertion. Fixed finger with one simple inner proximal seta, three simple inner distal and two on outer margin next to unguis, inner margin with three to four blunt denticles; dactylus marginally shorter than fixed finger, with one simple inner proximal seta.

Pereopod 1 (Figure 38G): coxa small, naked (not illustrated). Basis about three times as long as wide, about 1.7 times as long as merus, with three short setulose proximal setae. Ischium with two simple setae. Merus about 1.3 times as long as carpus, with two simple distal and one bipinnate setae. Carpus marginally shorter than propodus, about 1.9 times as long as wide, with two spiniform, three bipinnate, one spiniform- serrated distal and, six simple setae. Propodus as long as dactylus and unguis combined, about 2.7 times as long as wide, with one setulose medial, three simple, one pinnate, five bipinnate and one hook-like spiniform serrated setae. Dactylus with one simple proximal short seta; unguis naked.

Pereopod 2 (Figure 38H): articles with similar length to pereopod 1 except: basis marginally broader, about 2.2 times as long as wide, with two setulose proximal setae. Carpus about 1.5 times as long as merus. Propodus with six bipinnate and six simple setae. Dactylus marginally longer than propodus.

Pereopod 3 (Figure 38I): articles with similar length to pereopod 2 except: coxa with one setulose seta. Basis with three setulose setae. Carpus as long as propodus with seven simple setae. Propodus with five bipinnate setae. Dactylus about 1.4 times as long as propodus.

Pereopod 4 (Figure 38J): coxa absent. Basis as long as carpus and propodus combined, about 3.9 times as long as wide, with two setulose proximal setae. Ischium with two simple setae. Merus shortest, about 0.6 times as long as carpus, with one bipinnate and two simple distal setae. Carpus marginally longer than propodus and about 2.4 times as long as wide, with six bipinnate and five simple setae. Propodus half size of dactylus and unguis combined, with one setulose, six bipinnate and three simple setae. Dactylus with distal bilobate and finely serrated terminal shield at insertion of unguis; unguis slender, with two fine ventral rows of setae.

Pereopod 5 (Figure 38K): articles with similar length to pereopod 4 except: basis broader, about 2.5 times as long as wide. Carpus with twelve bipinnate and one simple fine distal setae. Propodus with seven bipinnate and three simple setae.

Pereopod 6 (Figure 38L): articles with similar length to pereopod 5 except: basis with one setulose proximal seta. Carpus with eight bipinnate and one simple fine distal setae.

Pleopods (Figure 37M): basal article short and stout, with three plumose setae. Exopod with about 17 plumose setae. Endopod with three inner and 15 outer plumose setae.

Uropod (Figure 36D): basal article naked, about 1.8 times as long as article 1 of endopod. Endopod with 14 articles. Articles 1–3 naked, subequal. Article 4 with one pair of plumose and other pair of simple setae. Article 5 with one simple seta. Article 6 with one plumose seta and three simple setae. Articles 7, 9 and 11–13 subequal, naked. Article 8 as article 4. Article 10 with one plumose and three simple setae. Article 14 one plumose, four simple setae and one aesthetasc. Exopod biarticulate, half the length of endopod article 1, with one simple seta on each article.

Manca II (Figure 36E, F). Body (Figure 36E) female paratype, length 2.2 mm, not calcified, about six times as long as wide; no apparent pigmentation, naked. Cephalothorax: as adult female. Cheliped (Figure 36F): sclerite rectangular. Basis about 1.2 times as long as wide, naked. No apparent ischium. Merus as adult female. Carpus with six simple dorsal and two ventral setae. Propodus with a distal margin very curved and pointed at tip, almost as reaching dactylus. Fixed finger and dactylus with similar setation as adult female paratype. Pereopods 1–6 (not illustrated) apparently as adult female but with less spiniform bipinnate setae on propodus. Uropods damaged.

Description. Copulatory male allotype.

Body (Figure 38A, B): heavily calcified, no apparent setae. Dorsoventrally flattened, about 8.1 times as long as wide. Cephalothorax: anterior margin relatively broad, widening posteriorly, about 2.2 times as long as wide and 1.2

times as long as the first three pereonites combined, naked, no apparent rostrum. Pereon: about 4.6 times as long as wide, about 49% of total body length. All pereonites pentagonal, no plumose or simple setae; pereonite 1 shortest, about 0.5 times as long as wide; pereonites 2 and 6 subequal, about 0.8 and 0.7 times as long as wide, respectively; pereonites 3–5 subequal, marginally longer than wide; pereonite 6 with two tiny genital cone (only one illustrated, Figure 38B). Pleon: about 2.3 times as long as wide, 24% of total body length. All pleonites subequal, lateral margin rounded, with one fine simple seta. Pleotelson (Figure 38C): marginally wider than long, naked.

Antennule (Figure 38D): article 1 longest, about 0.6 times as long as cephalothorax, about 6.6 times as long as wide, with one medial and four simple distal setae. Article 2 about 2.8 times as long as article 3, with one simple distal seta. Article 3 as long as articles 5 and 6 combined, naked. Article 4 rounded at basis bearing several long aesthetascs, about 2.6 times as long as wide. Articles 5 and 6 bearing one long aesthetasc each. Article 7 with three simple setae at tip.

Antenna (Figure 38E): about 0.8 times as long as antennule. Article 1 broader than following articles, about 1.8 times as long as wide, naked. Article 2 slender, about 5.7 times as long as wide, about 1.1 times as long as articles 3–5 combined, with one simple subdistal seta. Article 3 as long as article 7, with one simple distal seta. Article 4 marginally shorter than article 6, naked. Article 5 about 3.3 times as long as wide, with two plumose and a row (7–10) of subdistal setae. Article 6 about 0.8 times as long as articles 7–9 combined, with two simple distal setae. Articles 7 marginally longer than article 8, both naked. Article 9 shortest, with six simple distal setae.

Mouthparts and maxilliped: all reduced.

Cheliped (Figure 38B): sclerite rectangular, apparently naked. Basis stout. Ischium shaped as a narrow incomplete band extending from under the merus. Merus short, naked. Carpus long as in "robustus" group, but thinner and without protuberance or a long strong spine on ventral margin, about 1.9 times as long as cephalothorax, with two ventral simple setae. Propodus about 0.6 times as long carpus, about 4.8 times as long as wide, with two simple distal setae. Fixed finger reduced, with several blunt denticles on inner and outer margins bearing three and two simple setae, respectively. Dactylus long, about 2.6 times as long as fixed finger and slightly shorter than propodus (0.9 times), with a row of distal blunt denticles on inner and outer margins, naked.

Pleopods (Figure 38F): basal article about 1.2 times as long as wide, naked. Exopod with two apparent articles (at least a fusion line), article 1 with three small and one long plumose setae, article 2 with about 17 plumose setae. Endopod with about 16 inner and four plumose outer setae.

Uropod (Figure 38C): basal article attached mid-length on ventral margin. Endopod article 1 with several fine setae proximal to mid-length on outer margin, other articles missed. Exopod biarticulate, with two simple distal setae.

Remarks. *Venusticrus thor* n. sp. is the fourth described species of *Venusticrus* and the first record for the Pacific Ocean. The new species is similar its congeners in having characters such as: several dorsal setae on the cheliped carpus (more than ten), the type of armament on the dactylus at the unguis insertion of pereopods 4–6 (see Figure 38J–L), the cheliped propodus with a dorsodistal margin that is long, curved and pointed at its tip (also seen in *V. insolitus* and *V. rotermundiae*), and by the uropods attached mid-length on the ventral margin of the pleotelson— a diagnostic character for *Venusticrus*.

The females in the Neotanaidae family are known to have a very conservative morphology so often require a combination of characters to distinguish them. With the exception of *V. glandurus*, which differs from its congeners mainly due to the antennule article 1 and the number of plumose setae on the pereopods and uropods, the females of *V. rotermundiae* and *V. insolitus* share many characters with *V. thor*. However they can be separated from *V. thor* as this new species has the following unique character combination: body length about 7.9 times as long as wide (nine times in *V. insolitus* and *V. rotermundiae*); pleonal lateral epimera with three setae (one or two in *V. insolitus* and absent in *V. rotermundiae*), pleon with a very weak straight mid-ventral keel (pronounced and posteriorly directed in *V. glandurus* and *V. insolitus*); antennule article 1 about 2.9 times as long as wide (3.1 times in *V. insolitus* and 2.7 times in *V. rotermundiae*), with two simple and two plumose setae (with several setulose setae in *V. rotermundiae* and five simple setae in *V. insolitus*); maxilliped endite with five inner distal setulose spiniform setae (two in *V. insolitus* and three setulose spiniform and several tiny spiniform setae in *V. rotermundiae*), pereopods 1–6 number and type of seta; uropod basal article about 1.8 times as long as endopod article 1 (1.2 times in *V. glandurus*, 1.5 times and in *V. rotermundiae*); uropod exopod half size of endopod article 1 (1.5 times as long as endopod article 1 in *V. insolitus*, 0.8 in *V. rotermundiae* and 0.4 in *V. glandurus*).

The first record of a *Venusticrus* male was made by Gardiner (1975: 154) under the species *V. insolitus*. However, the author reported the male as non copulatory and just described the main characters without providing illustrations. The second record of a *Venusticrus* male was by Weigmann & Guerrero-Kommritz (2009: 28), when describing *V. rotermundiae*. The authors reported the specimen as damaged and lacking the chelipeds and accordingly did not illustrate or describe the specimen fully. To redeem this, a diagnosis and illustrations of a *Venusticrus* male are presented here. In addition, Weigmann & Guerrero-Kommritz (2009: 28), cited a "rudimental oostegites on pereopods 1 to 4" that was not found in the allotype of *V. thor*. Finally, a row of fine simple setae (about 8–10) was observed proximal to mid-length on the outer margin of the uropodal endopod article 1 (see Figures 33I and 38C). This character was previously found in *N. mesostenoceps* and *N. hadalis* and is well illustrated by Gardiner (1975: 69, fig. 27D; 75, fig. 32B, respectively). It is unclear if this character has been missed in other previous descriptions, hence should be carefully observed when describing new species of *Venusticrus* or *Neotanais*. All previous species of *Venusticrus* (including *V. rotermundiae*) were collected in the Atlantic Ocean, with the bathymetric distribution between 4460–5139 m.

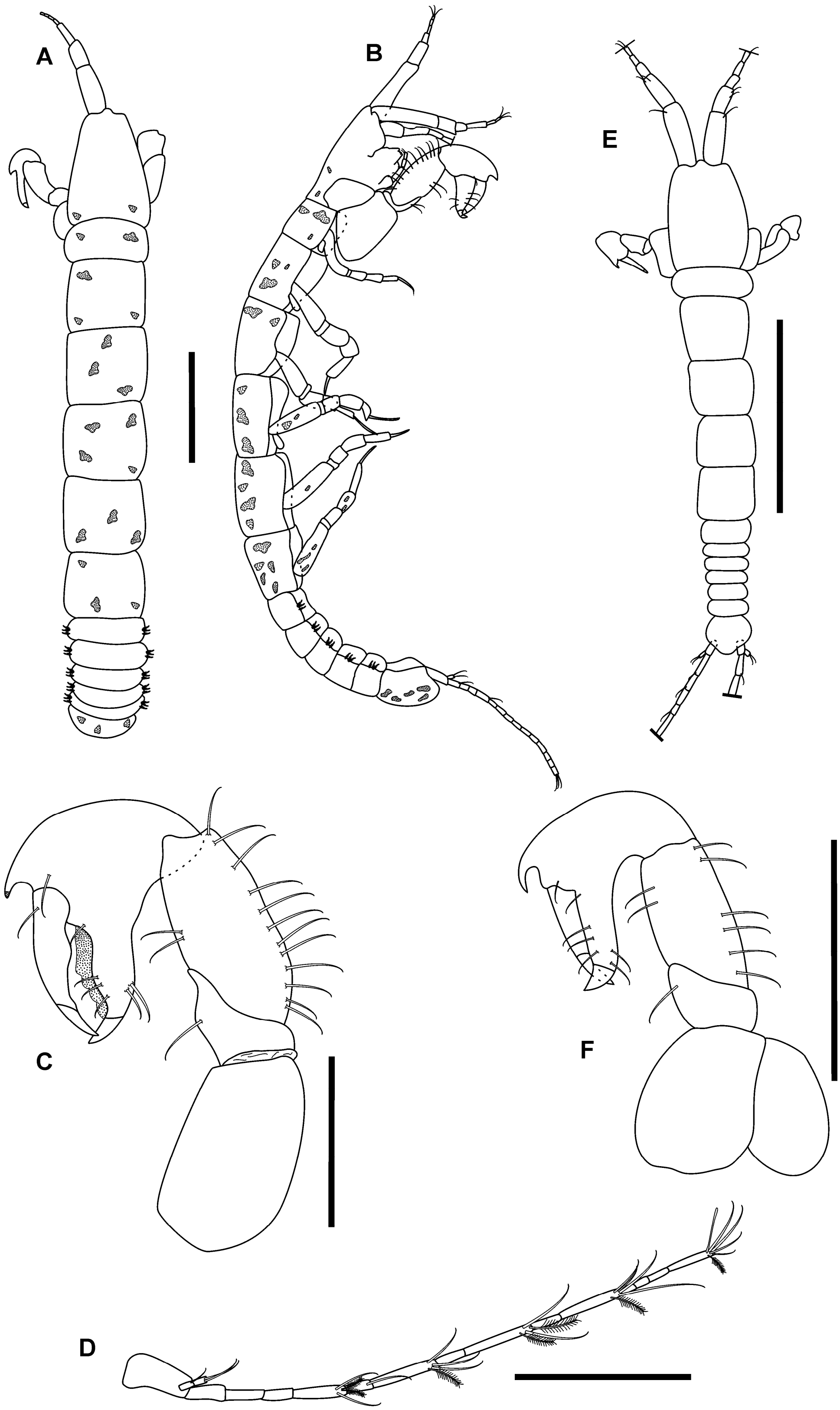


Figure 36. *Venusticrus thor* n. sp., female with oostegites (MNHN-IU-2014-10184): (A), holotype habitus dorsal view; (B), holotype habitus lateral view; female paratype (MNHN-IU-2014-10186): (C), cheliped; (D), uropod; manca female paratype (MNHN-IU-2014-10187): (E), habitus dorsal view; (F), cheliped. Scale bars: (A, B, E) = 1 mm; (C, D, F) = 0.5 mm.

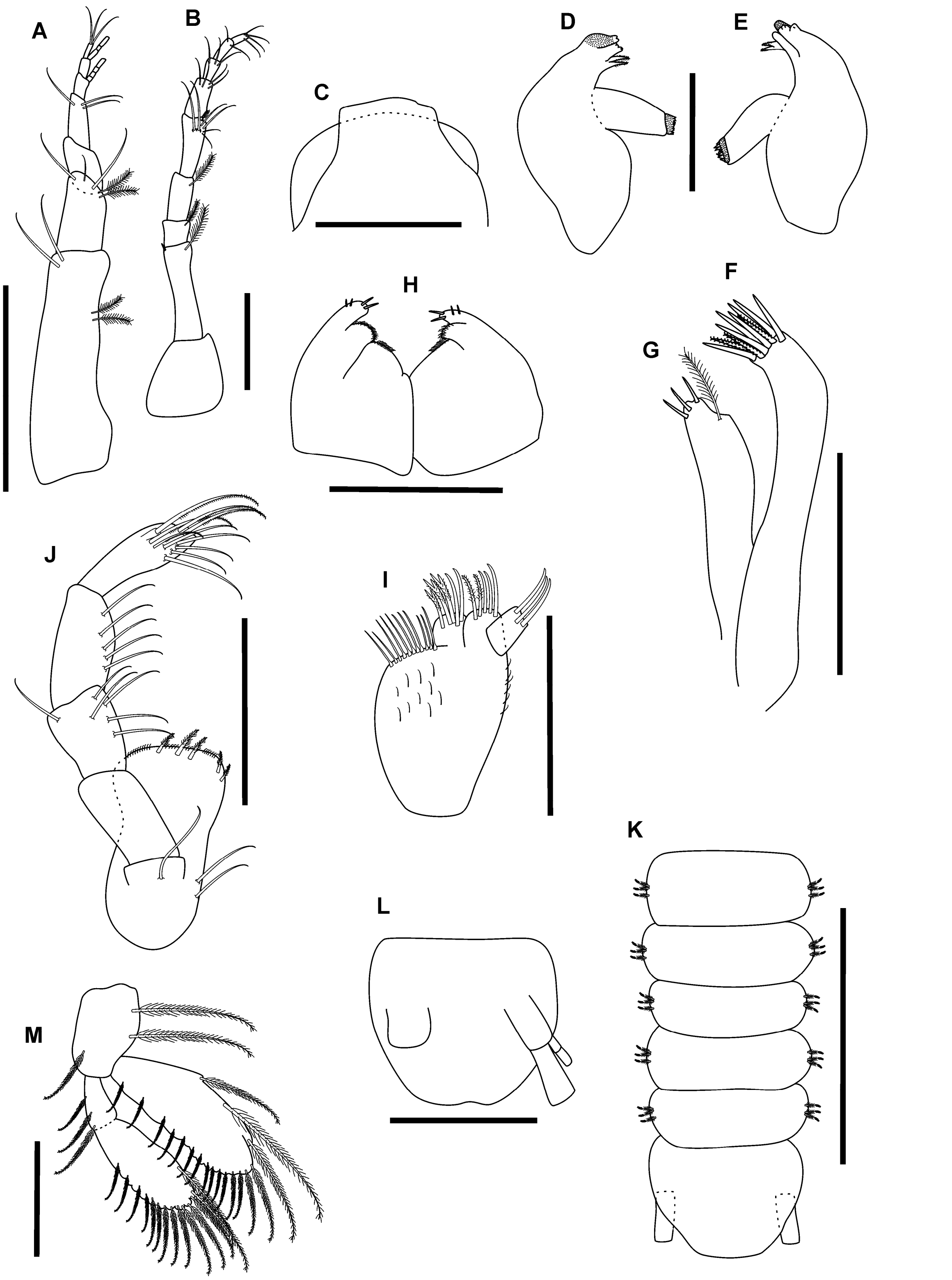


Figure 37. *Venusticrus thor* n. sp., female paratype: (A), antennule; (B), antenna; (C), labrum; (D), left mandible; (E), right mandible; (F), maxillule, outer endite; (G), maxillule, inner endite; (H), labium; (I), maxilla; (J), maxilliped; (K), pleon and pleotelson; (L), detail of pleotelson and uropod ventral attachment; (M), pleopod. Scale bars: (A, L) = 0.5 mm; (B–J), (M) = 0.2 mm; (K) = 1 mm.

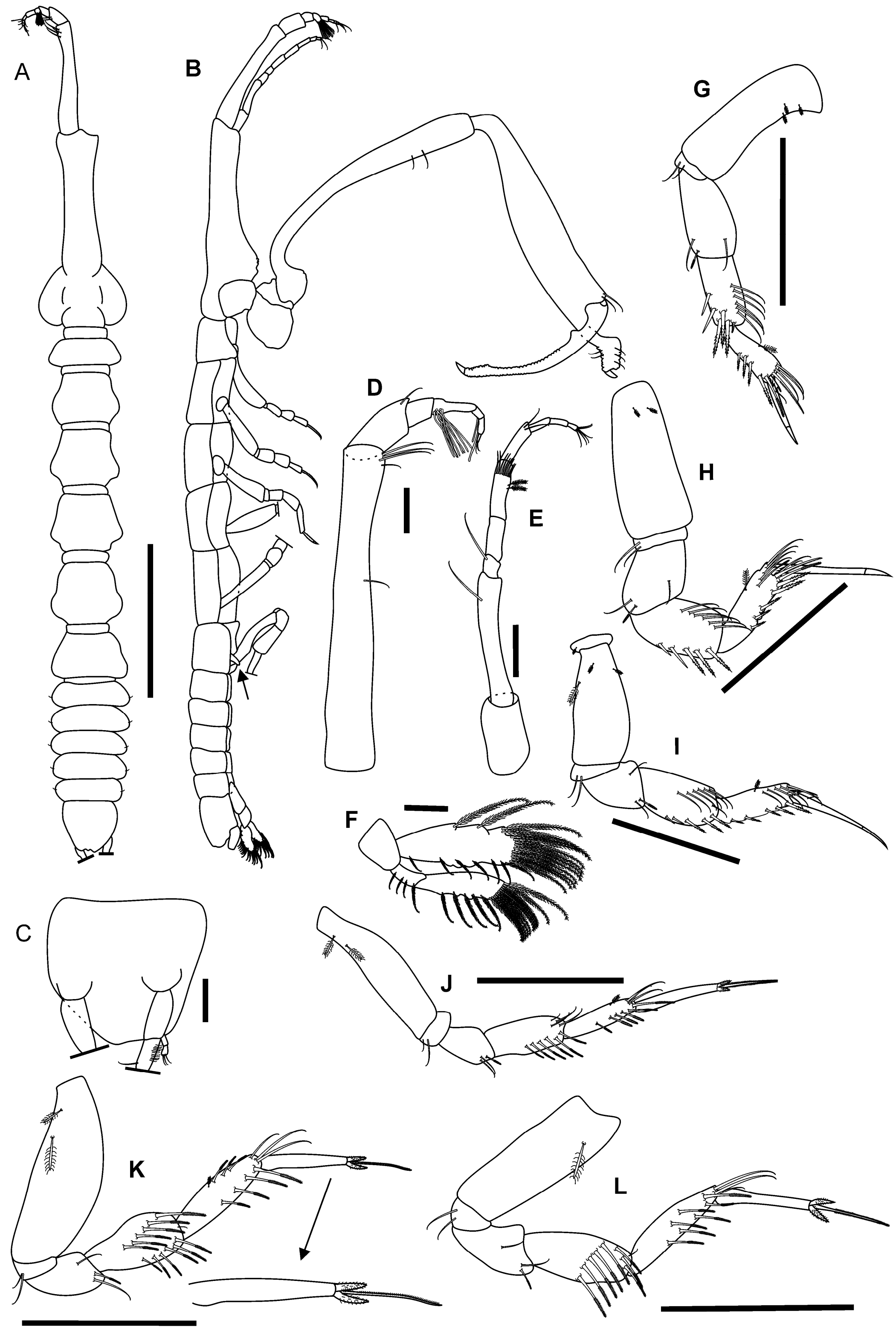


Figure 38. *Venusticrus thor* n. sp., copulatory male allotype (MNHN-IU-2014-10185): (A), habitus dorsal view; (B), habitus lateral view; (C), pleotelson and uropods; (D), antennule; (E), antenna; (F), pleopod; female paratype: (G), pereopod 1; (H), pereopod 2; (I), pereopod 3; (J), pereopod 4; (K), pereopod 5; (L), pereopod 6. Arrow in Fig. 6B indicates one of two genital cone. Scale bars: (A, B) = 2 mm; (C–F) = 0.2 mm; (G–L) = 0.5 mm.

Discussion

Gardiner (1975: 158) separated *Venusticrus* from the other three neotanaid genera *Carololangia*, *Herpotanais* and *Neotanais*, by some unusual characters such as the row of setae on the chelipedal merus, the cheliped bearing a large, thin, brown-bordered dorsal crest, the pleotelson acorn-shaped in dorsal view, the uropods attached midlength on ventral margin on the pleotelson, as well as other characters. Later, after a revision of genus *Neotanais*, Larsen (1999) transferred *V. insolitus* to *Venusticrus* due to its ventral pereopod and uropod attachments, setation of the cheliped carpus, and slim cheliped basis. In the present study we found additional characters that strongly support this transfer to *Venusticrus*. For instance, a consistent difference was observed between *Neotanais*, *Herpotanais*, *Carololangia* and *Venusticrus* regarding the armament at the dactylus of pereopods 4–6. The first three genera (at least where the species are properly described and illustrated) have a dactylus with a row of denticles arranged as a ring around the insertion of unguis (Figure 35D–F). In *Venusticrus*, the species have the previously-mentioned dactylus armament consisting of bilobate and finely serrated terminal shields at the insertion of the unguis (Figure 38J–L). Until now, this character has not been used for genus separation, but this study indicates that it might be a potential generic character and should be considered for further morphological analysis, since it is very conservative and easy to observe. Regarding the ventral uropod attachment, this character is found exclusively in the species of *Venusticrus*, possibly being an apomorphic character of this genus, while in *Neotanais*, *Herpotanais* and *Carololangia* the uropod is laterally attached.

Acknowledgments

This work is part of the senior author´s Ph.D. dissertation (CLAS), funded by CAPES—Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Grant number 5428/10–6). In addition, this research was partially supported by the European Regional Development Fund (ERDF) through the COMPETE—Operational Competitiveness Programme and national funds through FCT—Foundation for Science and Technology, under the project “PEst-C/MAR/LA0015/2013” "PEst-C/MAR/LA0015/2014". The authors are grateful to

Professor A. Brandt, University of Hamburg for allowing the use of the material from the ANDEEP cruises and to Dr. Graham Bird for identifying most of the ANDEEP material to genus level. Thanks are also extended to Drs Menot (IFREMER), to Rühlemann (BGR), chief scientists of the BIONOD expedition for inviting the junior author to participate in this cruise and for making the material available for study. We also thank to the editor Dr. Graham Bird and an anonymous referee who provided very constructive suggestions.

References

Anderson, G. (2013). Tanaidacea-Thirty Years of Scholarship (Vers. 1.0, May, 2013). Available from: http://peracarida.usm.edu/TanaidaceaText.htm (Accessed 14 Sept. 2015)

Bamber, R.N. (2007). Suborders Apseudomorpha Sieg, 1980 and Neotanaidomorpha Sieg, 1980. *In*: Larsen, K. & Shimomura, M. (eds.), Tanaidacea (Crustacea: Peracarida) from Japan III. The Deep Trenches: The Kurile-Kamchatka Trench and Japan Trench. *Zootaxa*, 1599: 13–40.

Beddard, F.E. (1886). Preliminary notice of the Isopoda collected during the voyage of HMS Challenger. Part III. *Proceedings of the Zoological Society of London*, 26: 97–122.

Dana, J.D. (1849). Conspectus Crustaceorum, Conspectus of the Crustacea of the U.S. *Exploring Expedition. American Journal of Science*, 2: 424–428.

Gardiner, L.F. (1975). The systematics, postmarsupial development and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea). *Smithsonian Contribution to Zoology*, 170: 1–265. http://dx.doi.org/10.5479/si.00810282.170

Holdich, D.M. & Jones, J.A. (1983). The distribution and ecology of British shallow-water tanaid crustaceans (Peracarida, Tanaidacea). *Journal of Natural History*, 17: 157–183. http://dx.doi.org/10.1080/00222938300770141

Johnson, S.B. & Attramadal, Y.G. (1982a). A functional morphological model of *Tanais cavolinii* Milne-Edwards (Crustacea, Tanaidacea) adapted to a tubicolous life-strategy. *Sarsia*, 67: 29–42.

Johnson, S.B. & Attramadal, Y.G. (1982b). Reproductive behaviour and larval development of *Tanais cavolinii* Milne-Edwards (Crustacea, Tanaidacea). *Marine Biology*, 71: 11–16.

Kakui, K., Katoh, T., Hiruta, S.F., Kobayashi, N. & Kajihara, H. (2011). Molecular Systematics of Tanaidacea (Crustacea: Peracarida) Based on 18S Sequence Data, with an Amendment of Suborder/Superfamily-Level Classification. *Zoological Science*, 28: 749–757. http://dx.doi.org/10.2108/zsj.28.749

Kudinova-Pasternak, R.K. (1970). Tanaidacea kurilo-kamciatkogo jeloba [Tanaidacea of the Kurile-Kamchatka Trench]. Trudy Instituta Okeanologii, *Transactions of the Institute of Oceanology*, 86: 341–381 (in Russian).

Kussakin, G.O. (1967). Faune Isopoda i Tanaidacea shelifovyh zon Antarkticheskih i Subantarkticheskih vod [Fauna of Isopoda and Tanaidacea in the Coastal Zones of the Antarctic and Subantarctic Waters]. Rezul'taty Biologicheskikh Issledovanii Sovetskoi Antarkticheskoi Ekspeditsii (1955–1958) [Biological Reports of the Soviet Antarctic Expedition (1955–1958)]. Issledovaniya Fauny Morei 4, 220–380 [Israel Program for Scientific Translations, Jerusalem, 1968].

Lang, K. (1949). Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologie*, 42: 1–14.

Lang, K. (1956). Neotanaidae nov. fam. with some remarks on the phylogeny of Tanaidacea. *Arkiv för Zoologie*, 9: 469–475.

Larsen, K. (1999). Deep-sea tanaidaceans (Crustacea: Peracarida) from the Albatross cruises 1885–86, with keys to the suborder Neotanaidomorpha. *Journal of Natural History*, 33: 1107–1132. http://dx.doi.org/10.1080/002229399299969

Larsen, K. (2003). Proposed new standardized terminology for tanaidacean Crustacea. *Journal of Crustacean Biology*, 23: 644–661. http://dx.doi.org/10.1651/C-2363

Larsen, K. (2005). Deep-sea Tanaidacea (Peracarida) from the Gulf of Mexico. Crustaceana Monographs 5. Brill, Leiden, 387 pp.

Larsen, K. & Araújo-Silva, C.L. (2014a). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited III: the family Akanthophoreidae. *Zootaxa*, 3796 (2): 237–264. http://dx.doi.org/10.11646/zootaxa.3796.2.2

Larsen, K. & Araújo-Silva, C.L. (2014b). A new genus of Colletteidae (Crustacea: Peracarida: Tanaidacea) from the Pacific with comments on dimorphic males with species specific characters. *Journal of the Marine Biological Association of the United Kingdom*, 94 (5): 969–974. http://dx.doi.org/10.1017/S0025315414000101

Larsen, K. & Błażewicz-Paszkowycz, M. (2003). A new species of *Neotanais* Beddard (Crustacea: Tanaidacea) from the Subantartctic [sic], off the Falkland Islands. *Zootaxa*, 339: 1–11.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny, the first step: the superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research*, 40: 205–222. http://dx.doi.org/10.1046/j.1439-0469.2002.00193.x

Larsen, K., Tuya, F. & Froufe, E. (2014). Genetic divergence of tanaidaceans (Crustacea: Peracarida) with low dispersal ability. *Scientia Marina*, 78: 81–90. http://dx.doi.org/10.3989/scimar.03878.19A

Mendoza, J.A. (1982). Some aspects of the autecology of *Leptochelia dubia* (Krøyer, 1842) (Tanaidacea). *Crustaceana*, 43: 225–240. http://dx.doi.org/10.1163/156854082X00164

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzieger*, 205: 401–416.

Thistle, D., Yingst, J.Y. & Fauchald, K. (1985). A deep-sea benthic community exposed to strong near–bottom currents on the Scotland Rise (western Atlantic). *Marine Geology*, 66: 91–112. http://dx.doi.org/10.1016/0025-3227(85)90024-6

Weigmann, S. & Guerrero-Kommritz, J. (2009). New species of *Neotanais* Beddard, 1886 (Crustacea, Tanaidacea) from the deep sea of the tropical and southern East Atlantic Ocean. *Zootaxa*, 1992: 20–36.

Wi, J.H., Suh, H.L. & Yu, O.H. (2014). Two new species of the deep-sea genus *Neotanais* Beddard, 1886 (Tanaidacea: Neotanaididae) from the Eastern Central Pacific. *Journal of Crustacean Biology*, 34: 875–885. http://dx.doi.org/10.1163/1937240X-00002274

Wi, J.H., Suh, H.L. & Yu, O.H. (2015). Description of two new species of Neotanais Beddard, 1886 (Crustacea, Tanaidacea) from KODOS area. *Zootaxa*, 3926 (2): 244–256. http://dx.doi.org/10.11646/zootaxa.3926.2.5

Wolff, T. (1956a). *Crustacea Tanaidacea from depths exceeding 6000 meters. In*: Bruun, A., Greve, S., Spärck, R. & Wolff, T. (eds.), Galathea Report: Scientific Results of the Danish Deep-Sea Expedition Round the World 1950-52, Vol. 2. Danish Science Press, Copenhagen. pp. 187–241.

Wolff, T. (1956b). Six new abyssal species of *Neotanais* (Crustacea, Tanaidacea). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København*, 118: 41–52.

http://dx.doi.org/10.11646/zootaxa.4018.4.3

http://zoobank.org/urn:lsid:zoobank.org:pub:A297C919-7B2B-482E-A3FD-97CD53C9B3EB

Zootaxa, 3796 (2): 237–264 (2014)

Article 6. The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited III: the family Akanthophoreidae

Kim Larsen[1] & Catarina L. Araújo-Silva[1,2]

[1]Aquatic Ecology and Evolution Department, CIIMAR (Centro Interdisciplinar de Investigação Marinha e Ambiental), Rua dos Bragas, 289, 4050–123 Porto, Portugal. [2]Capes Foundation, Ministry of Education of Brazil, Brasília–DF, 70040–020, Brazil. E-mail: tanaids@hotmail.com; katelas@hotmail.com

Abstract

A restricted phylogenetic analysis is conducted to test if the family Akanthophoreidae is monophyletic. The family was found to be monophyletic with a Bremer support of 11 and is redefined to include the genera *Akanthophoreus*, *Chauliopleona*, *Mimicarhaphura*, *Parakanthophoreus* gen. nov., *Paraleptognathia*, *Stenotanais*, and *Tumidochelia*, while *Gejavis* is removed. *Akanthophoreus* and *Paraleptognathia* are redefined and now consist of only four and two species respectively. The remaining species previously assigned to these genera are transferred to a new genus *Parakanthophoreus*. A key to the genera of the family is presented. Two new species of *Chauliopleona*, *C. ciimari* and *C. andeepi*, and one of *Parakanthophoreus*, *P. greenwichius*, are described from the ANDEEP I–III and ANDEEP-SYSTCO material.

Key words: ANDEEP I–III, ANDEEP-SYSTCO, Tanaidacea, Tanaidomorpha, Akanthophoreidae, *Parakanthophoreus*, Antarctica, Restricted-phylogeny.

Introduction

The ANDEEP (ANtarctic benthic DEEP-sea biodiversity) collections obtained from cruises conducted by the University of Hamburg and the Senckenberg Institute in 2002, 2005, and 2007 (ANDEEP I–III and ANDEEPSYSTCO), have revealed much tanaidacean material that remains to be examined. This is the third paper from this re-examination, the first two concerning the families Agathotanaidae Lang, 1971 (Larsen *et al*. 2013), Anarthruridae Lang, 1971, and *incertae sedis* (Larsen 2013) while this study focuses on the family Akanthophoreidae Sieg, 1986. An overview of previous tanaidacean studies of the ANDEEP material can be found in Larsen (2013) and references herein.

The first family level name (subfamily) was established by Sieg, 1986. Recently Błażewicz-Paszkowycz & Bamber (2011) elevated the subfamily Akanthophoreinae to full (monotypic) family status and later *Chauliopleona* Dojiri & Sieg, 1997 was included in this family (Błażewicz-Paszkowycz, Bamber & Jóźwiak 2013). However, the diagnosis (Błażewicz-Paszkowycz & Bamber 2011: 25) is almost identical with that of Sieg´s (1986) diagnosis of the anarthrurid subfamily Akanthophoreinae, with a few omissions to adjust for genera since removed from this taxon. Sieg´s (1986) diagnosis is at best insufficient and in some places erroneous and so a reappraisal is needed.

No tanaidacean worker would dispute that the phylogeny and systematics of the order is unresolved. At the same time, all attempts to construct an all-encompassing phylogeny have failed to provide much resolution owing to excessive character reversals, high numbers of taxa, and a general lack of stable characters. A phylogenetic analysis by Guerrero-Kommritz & Brandt (2005) showed a clear affinity between *Chauliopleona* and *Paraleptognathia* Kudinova-Pasternak, 1981 (including *Akanthophoreus* Sieg, 1986 which at that time was synonymized with *Paraleptognathia*), suggesting a 'generic cluster'. A restricted phylogeny' (see Bird & Larsen 2009) is conducted here to examine such a relationship.

This paper also describes three new species of Akanthophoreidae: one of *Parakanthophoreus* and two of *Chauliopleona*, from the Subantarctic-Antarctic region. New records of *C. nickeli* Guerrero-Kommritz, 2005 are also included.

Material and Methods

The material is deposited in the Natural History Museum, Hamburg, Germany and was collected during the ANDEEP expeditions in 2002, 2005, and 2007. The material was sieved over a 0.5 mm sieve and immediately fixed in 95% alcohol.

Dissections were made in glycerine using chemically sharpened tungsten wire needles. Body length was measured from the tip of the cephalothorax to the apex of the pleotelson in lateral view to avoid bias from body curvature. The terminology in the descriptions is based on Larsen (2003). Adjectives such as long and short are used as relative qualifiers in respect of the appendage being described.

The restricted phylogenetic analysis was performed as described by Bird & Larsen (2009) using TNT (Goloboff *et al*. 2008). While TNT only operate with one designated outgroup (here chosen as Teleotanaidae, currently regarded as the most ‘plesiomorphic’ paratanaoidean family in the analysis by Bird & Larsen (2009)), all the 16 ‘non-Akanthophoreidae’ taxa function in reality as outgroup taxa (each scored as a composite) since this is a restricted analysis which only aims at solving the validity of the Akanthophoreidae, not the internal relationships between other tanaidacean families. For the same reason, 22 characters are parsimony-uninformative but function as outgroup-defining characters. Most of the characters correspond to those used in the earlier Bird & Larsen phylogeny to preserve some consistency here but it accepted that new insights will eventually require some revision of these.

The ingroup is made up of eight taxa, representing taxa suspected or suggested to belong to the Akanthophoreidae. The data consist of 103 unordered and unweighted characters of which 71 are parsimony informative. Unless otherwise stated the characters are scored from females only. The settings used were: Data format = 8 states; memory, max tree = 10.000; collapsing rule min. length = 0; traditional search with ‘Collapse trees after search’ and ‘Tree Bisection Reconnection’ on; Traditional Search; ‘retain 100 trees per round’; 1000 replications. The consensus is calculated from 160 shortest trees with a tree length of 255. The Bremer support (Bremer 1994) was used to estimate branch support and the values are given next to the branches in Figure 39. The Bremer support analysis was performed using a 12-step suboptimal tree search’, with a relative fit value of 1.00, values are given in absolute numbers.

Many phylogeneticists would argue that the inclusion of more taxa from the incertae sedis (floaters) group might alter the tree topography. To pre-empt such criticisms, we argue that such a process is contrary to the purpose of a ‘restricted phylogeny’. The addition of all floaters would (and did during a previous attempts) reduced the resolution of the tree. However, even with a large number of floaters included, the monophyletic nature of the Akanthophoreidae, with the genera mentioned above, remained consistent.

Character description. For data matrix see Appendix I.

0 Compound eyes (0 = absent, 1 = present). This character corresponds to character ‘8’ from Bird & Larsen (2009) and character ‘5’ from Larsen & Wilson (2002). Outgroup-defining character.

1 Cephalothorax narrower anteriorly (0 = absent, 1 = present). This character corresponds to character ‘9’ from Bird & Larsen (2009).

2 Pereon short and stout l/w ratio < 2.5 (0 = absent, 1 = present). This character corresponds to character ‘11’ from Bird & Larsen (2009). This character is typically seen in Pseudotanaidae Sieg and certain species of Typhlotanaidae Sieg. Outgroup-defining character.

3 Pereonites 1–3 very short relative to pereonites 4–6 (0 = absent, 1 = present). This character corresponds to character ‘12’ from Bird & Larsen (2009) and characters ‘3’ and ‘41’ in Larsen & Wilson (2002). Outgroupdefining character.

4 Pereonite 1 trapezoidal (wider anterior) (0 = absent, 1 = present). This character corresponds to character ‘13’ from Bird & Larsen (2009).

5 Pereonite 1 hyposphenian/sternal spur (0 = absent, 1 = present). This character corresponds to character ‘14’ from Bird & Larsen (2009). Outgroup-defining character.

6 Pleon expansion (0 = absent, 1 = present). This character is only found in the parasitic family Mirandotanaidae Błażewicz-Paszkowycz & Bamber, 2009 and the floater *Exspina*. Outgroup-defining character.

7 Pleon fusion (any type) (0 = absent, 1 = present). This character corresponds to character ‘9’ from Larsen & Wilson (2002). Outgroup-defining character.

8 Pleon narrower than pereon (0 = absent, 1 = present). This character corresponds to character ‘6’ from Larsen & Wilson (2002). Outgroup-defining character.

9 Pleon reduced (0 = absent, 1 = present). This character corresponds to character ‘15’ from Bird & Larsen (2009). Outgroup-defining character.

10 Pleonite lateral setae circumplumose (0 = absent, 1 = present). This character corresponds to character ‘16’ from Bird & Larsen (2009) and character ‘8’ from Larsen & Wilson (2002). Outgroup-defining character.

11 Pleonite 5 ventral, posteriorly directed, spur (0 = absent, 1 = present). The present state is restricted to the genus *Chauliopleona*.

12 Pleotelson lateral spurs (0 = absent, 1 = present). The present state is restricted to the genus *Akanthophoreus*.

13 Antennule article 1 composite (0 = absent, 1 = present). This character corresponds to character ‘19’ from Bird & Larsen (2009).

14 Antennule short penultimate article (0 = absent, 1 = article 2, 2 = article 3). This character corresponds to character ‘20’ from Bird & Larsen (2009).

15 Antennule terminal article minute, cap-like (0 = absent, 1 = present). This character corresponds to character ‘21’ from Bird & Larsen (2009).

16 Antennule article 3 subterminal aesthetascs (0 = absent, 1 = present). This character corresponds to character ‘22’ from Bird & Larsen (2009).

17 Antenna multi-articled, count (0 = seven, 1 = six, 2 = less than six). This character corresponds to character ‘26’ from Bird & Larsen (2009) and ‘14’ from Larsen & Wilson (2002).

18 Antenna article 2 larger or longer than article 3 (0 = absent, 1 = present). This character corresponds to character ‘27’ from Bird & Larsen (2009).

19 Antenna article 2 dorsal strong acute spiniform seta/apophysis (0 = absent, 1 = present). This character corresponds to character ‘29’ from Bird & Larsen (2009).

20 Antenna article 2 dorsal stout broad-based spiniform seta (0 = absent, 1 = present). This character corresponds to character ‘30’ from Bird & Larsen (2009).

21 Antenna article 2 ventral strong acute spiniform seta or apophysis with seta (0 = absent, 1 = spiniform seta, 2 = apophysis). This character corresponds to character ‘31’ from Bird & Larsen (2009).

22 Antenna article 3 dorsal strong acute spiniform seta/apophysis (0 = absent, 1 = present). This character corresponds to character ‘32’ from Bird & Larsen (2009) and ‘13’ from Larsen & Wilson (2002).

23 Antenna article 3 dorsal strong broad-based spiniform seta (0 = absent, 1 = present). This character corresponds to character ‘33’ from Bird & Larsen (2009).

24 Labial lobes pairs, count (0 = two, 1 = one). This character corresponds to character '34' from Bird & Larsen (2009) and '21' from Larsen & Wilson (2002). Outgroup-defining character. It has to be mentioned that several forms of vestigial lobes can be found in various taxa but only the true form is scored here since the vestigial forms would be too hard to score with sufficient level of confidence.

25 Labial medial spiniform setae (0 = absent, 1 = present). This character is only found in the family Agathotanaidae. Outgroup defining character.

26 Mandible molar broad, grinding surface (0 = absent, 1 = present). This character corresponds to character '35' from Bird & Larsen (2009) and '17' from Larsen & Wilson (2002).

27 Mandible molar shape (0 = grinding, 1 = broad nodulose, 2 = broad spinose, 3 = acuminate-armed, 4 = acuminate-simple, 5 = reduced/absent). This character corresponds to character '36' from Bird & Larsen (2009) and '17' from Larsen & Wilson (2002).

28 Mandible right incisor bifid—points open/symmetrical, with distal crenulations (0 = absent, 1 = present). This character corresponds to character '37' from Bird & Larsen (2009).

29 Mandible right incisor bifid—points closed/asymmetrical (0 = absent, 1 = present). This character corresponds to character '38' from Bird & Larsen (2009).

30 Mandible left incisor/lacinia broad, facing anterior (0 = absent, 1 = present). This character corresponds to character '39' from Bird & Larsen (2009).

31 Maxillule palp distally bent (near or actual right-angle) (0 = absent, 1 = present). This character corresponds to character '40' from Bird & Larsen (2009).

32 Maxillule endite terminal spiniform setae short (0 = absent, 1 = present). This character corresponds to character '41' from Bird & Larsen (2009). Outgroup-defining character.

33 Maxilla modified (0 = absent, 1 = present). The absent state (a reduced and ovoid maxilla) is most common within the Paratanaoidea, but a number of genera (within the family Akanthophoreidae) have a much better developed maxilla with a broad basis, almost as long as the maxillule endite, and mandibles. Often weak crenulations or setae are also present.

34 Maxilliped basis and endites both laterally expanded (0 = absent, 1 = present). This character corresponds to character '42' from Bird & Larsen (2009) and '33' from Larsen & Wilson (2002).

35 Maxilliped basis fusion (0 = absent, 1 = present). This character corresponds to character ‘43’ from Bird & Larsen (2009) and ‘31’ from Larsen & Wilson (2002).

36 Maxilliped endite fusion (0 = absent, 1 = present, 2 = present in part). This character corresponds to character ‘44’ from Bird & Larsen (2009) and ‘32’ from Larsen & Wilson (2002).

37 Maxilliped endites distally expanded or flared (0 = absent, 1 = weak, 2 = strong, 3 = highly developed). This character corresponds to character ‘45’ from Bird & Larsen (2009) and ‘33’ from Larsen & Wilson (2002).

38 Maxilliped endite marginal blunt seta/teeth, count (0 = four, 1 = three, 2 = one, 3 = absent, 4 = two). This character corresponds to character ‘46’ from Bird & Larsen (2009) and ‘34’ from Larsen & Wilson (2002).

39 Maxilliped endite marginal spiniform setae, count (0 = five, 1 = four, 2 = three, 3 = one, 4 = absent). This character corresponds to character ‘47’ from Bird & Larsen (2009).

40 Maxilliped endite paired rounded spiniform setae/tubercles (marginal or submarginal) (0 = absent, 1 = present, 2 = unarticulated rounded cusp). This character corresponds to character ‘48’ from Bird & Larsen (2009) but with the additional state 2.

41 Maxilliped endite large lateral seta (0 = absent, 1 = present). This character corresponds to character ‘49’ from Bird & Larsen (2009).

42 Maxilliped basal setae, count (0 = three or more, 1 = two, 2 = one, 3 = absent). This character corresponds to character ‘50’ from Bird & Larsen (2009).

43 Maxilliped palp article 2 lateral seta (0 = absent, 1 = present). This character corresponds to character ‘51’ from Bird & Larsen (2009).

44 Maxilliped palp article 2 with bifid/trifid/strongly pectinate spiniform seta (0 = absent, 1 = present). This character corresponds to character ‘52’ from Bird & Larsen (2009).

45 Maxilliped palp article 2 long seta (as long as articles 3–4) (0 = absent, 1 = present). This character corresponds to character ‘53’ from Bird & Larsen (2009).

46 Maxilliped palp article 2 medial setae, count (0 = four or more, 1 = three, 2 = two). This character corresponds to character ‘54’ from Bird & Larsen (2009).

47 Maxilliped palp article 3 medial setae, count (0 = five or more, 1 = three or four). This character corresponds to character ‘55’ from Bird & Larsen (2009).

48 Cheliped-cephalothorax sclerite dorsally inserted (triangular) on basis (0 = absent, 1 = present). This character corresponds to character '56' from Bird & Larsen (2009) and '38' from Larsen & Wilson (2002).

49 Cheliped basis with suture ('pseudocoxa') (0 = absent, 1 = present). This character corresponds to character '57' from Bird & Larsen (2009). Outgroup-defining character found in *Nesotanais* and Anarthruridae (but these may not be equivalent, i.e. homoplastic).

50 Cheliped basis reaches pereonite 1 (0 = absent, 1 = present). This character corresponds to character '58' from Bird & Larsen (2009).

51 Cheliped carpus shield (0 = absent, 1 = present). This character is present in many genera but not all species, which are here shown to belong to Akanthophoreidae. However, it may also be found in other taxa currently considered 'floaters'.

52 Cheliped carpus stout, rounded (as long as broad) (0 = absent, 1 = present). This character corresponds to character '59' from Bird & Larsen (2009).

53 Cheliped carpus and propodus with heavy ornamentation (0 = absent, 1 = present). This character is one of the two controversial points in the synonymisation of *Akanthophoreus* with *Paraleptognathia* by Guerrero-Kommritz (2004) and the rejection of same by Bird (2007).

54 Cheliped propodal fixed finger proximal denticulation (0 = absent, 1 = present). See previous character.

55 Cheliped chela with elongated fixed finger and dactylus (0 = absent, 1 = present). The 'present' state now includes all expressions of an elongated fixed finger/dactylus found in taxa such as Pseudotanaidae and Leptognathiidae.

56 Cheliped fixed-finger crushing incisive margin (0 = absent, 1 = present). This character corresponds to character '62' from Bird & Larsen (2009).

57 Cheliped dactylus crenulations (0 = absent, 1 = present). This character corresponds to character '63' from Bird & Larsen (2009).

58 Cheliped propodus ventral setae, count (0 = three or more, 1 = two, 2 = one). This character corresponds to character '65' from Bird & Larsen (2009).

59 Cheliped carpus mid-ventral setae, count (0 = three, 1 = two, 2 = one, 3 = none). This character corresponds to character '67' from Bird & Larsen (2009).

60 Cheliped merus ventral setae, count (0 = four or more, 1 = three, 2 = two, 3 = one). This character corresponds to character '68' from Bird & Larsen (2009).

61 Pereopod 1 bayonet spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘69’ from Bird & Larsen (2009).

62 Pereopod 1 propodus with ventrodistal setation (0 = absent, 1 = simple seta, 2 = spiniform seta). This character corresponds to character ‘70’ from Bird & Larsen (2009).

63 Pereopod 1 dactylus/unguis clearly longer than propodus (0 = absent, 1 = present). This character corresponds to character ‘71’ from Bird & Larsen (2009) and ‘44’ from Larsen & Wilson (2002).

64 Pereopod 1 unguis longer than dactylus (0 = absent, 1 = present). This character corresponds to character ‘72’ from Bird & Larsen (2009) and ‘44’ from Larsen & Wilson (2002).

65 Pereopod 1 and pereopods 2–3 different in shape and setal arrangement (0 = absent/weak, 1 = moderate, 2 = strong). This character corresponds to character ‘73’ from Bird & Larsen (2009).

66 Pereopods 2–3 merus simple, stout or short spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘74’ from Bird & Larsen (2009).

67 Pereopods 2–3 merus bayonet spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘75’ from Bird & Larsen (2009).

68 Pereopods 2–3 carpus bayonet spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘76’ from Bird & Larsen (2009).

69 Pereopods 2–3 carpus blade-like spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘77’ from Bird & Larsen (2009). Outgroup-defining character.

70 Pereopods 2–3 carpus spiniform setae, count (0 = none, 1 = one, 2 = two or more). This character corresponds to character ‘78’ from Bird & Larsen (2009).

71 Pereopods 2–3 carpus two ventrodistal spiniform setae only (0 = absent; 1 = present, one type; 2 = present, two types). This character corresponds to character ‘81’ from Bird & Larsen (2009).

72 Pereopods 2–3 propodus ventrodistal seta (0 = absent, 1 = simple seta, 2 = spiniform seta). This character corresponds to character ‘79’ from Bird & Larsen (2009).

73 Marsupium structure (0 = four pairs, 1 = one pair). This character corresponds to character ‘41’ from Larsen & Wilson (2002).

74 Pereopods 4–6 coxa (0 = fused, 1 = unfused). This character corresponds to character ‘47’ from Larsen & Wilson (2002). Only those taxa which unambiguously display the coxa are scored with the ‘present’ state as there are many examples of partly fused coxa.

75 Pereopods 4–6 basis thicker than pereopods 1–3 basis (≥ two thirds longer than broad) (0 = absent, 1 = present, 2 = thinner). This character is modified from character ‘83’ from Bird & Larsen (2009).

76 Pereopods 4–6 basis stout (≤ 2.5 times longer than broad) (0 = absent, 1 = present). This character corresponds to character ‘84’ from Bird & Larsen (2009).

77 Pereopods 4–6 merus setae (0 = absent, 1 = simple, 2 = robust, 3 = bayonet). This character corresponds to character ‘85’ from Bird & Larsen (2009).

78 Pereopods 4–6 carpus microtrichial field or ‘prickly tubercle’ (with or without microtrichia) (0 = absent, 1 = microtrichia, 2 = microtrichia, strong, 3 = prickly tubercle). This character corresponds to character ‘86’ from Bird & Larsen (2009). Outgroup-defining character.

79 Pereopods 4–6 carpus bayonet setae (0 = absent, 1 = present). This character corresponds to character ‘87’ from Bird & Larsen (2009).

80 Pereopods 4–6 carpus complex-denticulate, or hook-like, spiniform setae (0 = absent, 1 = complex, 2 = hooks). This character corresponds to character ‘88’ from Bird & Larsen (2009).

81 Pereopods 4–6 carpus blade-like setae (0 = absent, 1 = present). This character corresponds to character ‘89’ from Bird & Larsen (2009). Outgroup-defining character.

82 Pereopods 4–6 carpus spiniform setae, count (0 = one, 1 = two, 2 = three, 3 = four, 4 = none). This character is modified from character ‘90’ in Bird & Larsen (2009).

83 Pereopods 4–6 dorsomedial pinnate setae (0 = absent, 1 = present). This character corresponds to character ‘91’ from Bird & Larsen (2009).

84 Pereopods 4–5 propodus dorsodistal setae, count (0 = four or more, 1 = three, 2 = two, 3 = one). This character corresponds to character ‘92’ from Bird & Larsen (2009).

85 Pereopod 6 propodus dorsodistal setae, count (0 = four or more, 1 = three, 2 = two, 3 = one). This character corresponds to character ‘96’ from Bird & Larsen (2009).

86 Pereopods 1–3 carpus with rod, or bone-like seta (0 = absent, 1 = present). This character corresponds to character '97' from Bird & Larsen (2009).

87 Pereopods 4–6 rod, or bone-like seta (0 = absent, 1 = present). This character corresponds to character '98' from Bird & Larsen (2009).

88 Pereopods 4–6 dactylus-unguis 'claw-like' (0 = absent, 1 = present). This character corresponds to character '99' from Bird & Larsen (2009) and '46' from Larsen & Wilson (2002). Outgroup defining character.

89 Pereopods 4–6 unguis tip modified (0 = absent, 1 = present). This character corresponds to character '100' from Bird & Larsen (2009).

90 Pleopod basal article inner setae (0 = absent, 1 = present). This character corresponds to character '102' from Bird & Larsen (2009).

91 Pleopod endopod setae all terminal (0 = absent, 1 = present). This character corresponds to character '103' from Bird & Larsen (2009).

92 Pleopod exopod setae all terminal (0 = absent, 1 = present). This character corresponds to character '104' from Bird & Larsen (2009).

93 Pleopod endopod inner/subterminal setae, count (0 = absent, 1 = one, 2 = two or more). This character corresponds to character '105' from Bird & Larsen (2009).

94 Uropod endopod articles, count (0 = five to seven, 1 = three to four, 2 = two, 3 = one, 4 = fused with basal article). This character corresponds to character '106' from Bird & Larsen (2009) and '51' from Larsen & Wilson (2002).

95 Uropodal exopod fused with basal article (0 = absent, 1 = present and naked, 2 = present and with setae). The various states are found within several families as Agathotanaidae, Anarthruridae, and Tanaellidae Larsen & Wilson, 2002. It is not to be confused with character 102 which deals with an accessory uropodal spur and it almost certainly homoplastic across the families mentioned.

96 Uropodal endopod spur (0 = absent, 1 = present). This character is so far only found in the genus *Mimicarhaphura* Sieg, 1986.

97 Uropod exopod articles (0 = absent, 1 = one, 2 = two). This character corresponds to character '52' from Larsen & Wilson (2002). Outgroup-defining character.

98 Uropod endopod length (0 = longer than pleotelson, 1 = shorter than pleotelson). This is a character that, despite some homoplasy, holds promise of phylogenetic information.

99 Uropod endopod thin (0 = absent, 1 = present). The ‘present’ state means at least 3.5 times as long as wide. This is a novel character that seems stable in most families.

100 Uropod exopod length (0 = longer than first endopod article, 1 = shorter than first endopod article, 2 = fused to basal article). This is a novel, for a phylogenetic study, character that is polymorphic in several families but may still contain important phylogenetic information.

101 Non-feeding male (0 = absent, 1 = present). This character corresponds to a restricted form of character ‘4’ from Larsen & Wilson (2002).

102 Uropodal basal article [with exopod] spur (0 = absent, 1 = present). This spur is not homologous with the fused exopod mentioned under character 94. It is currently only recorded in the genera *Kanikipa* Bird, 2011, *Tumidochelia* Knight *et al*., 2003, and one species of Colletteidae Larsen & Wilson, 2002 (i.e. *Leptognathiella spinicauda* Bird & Holdich, 1984).

Results

The analysis conducted in this paper supports the monophyletic nature of Akanthophoreidae with the addition of the following genera currently assigned as incertae sedis: *Mimicarhaphura*, *Paraleptognathia*, *Stenotanais*, and *Tumidochelia*, as well as the new genus *Parakanthophoreus*, but not *Gejavis* Błażewicz-Paszkowycz & Bamber (2012) as suggested by those authors.

Systematics

Order Tanaidacea Dana, 1849

Suborder Tanaidomorpha Sieg, 1980

Superfamily Paratanaoidea Lang, 1949

Family Akanthophoreidae Sieg, 1986

Type-genus. *Akanthophoreus* Sieg, 1986.

Diagnosis (modified after Sieg (1986) and Błażewicz-Paszkowycz & Bamber (2011)). Female. Antennule four-articled with discrete or fused terminal cap-like article (character 13, state 0/1). Mandibular molar-process tapering to thin, denticulate tip (character 26, state 0; character 27, state 3). Maxilla as large as or larger than labium (character 33, state 1), with a wide basis, tapering distally, often with setules. Labium with one pair of lobes but often with visible rudiments of outer lobes (character 24, state 1). Maxilliped palp article 2 with outer seta (character 43, state 1). Cheliped attached via elongated sclerite (character 48, state 1); carpus often with large ventral shield (character 51, state 0/1); chela flared, propodus, fixed finger and dactylus often with dorsal crenulations (character 57, state 0/1). All pereopod meri and carpi with slender bayonet-shaped spiniform setae (characters 61, 67, and 79, state 1). Pereopods 2 and 3 merus and carpus not compact, carpus longer than merus (character 24, state 1), propodus not ventrally convex and with row of small ventral spines (character 13, state 0/1). Pereopods 4–6 coxa absent (character 74, state 0), propodus with fine setules/spinules, dactylus elongate, grooved with finely setules/spinules on two edges, not fused with unguis (character 88, state 0). Uropod biramous, endopod with two elongated articles (character 94, state 2) combined longer than pleotelson, exopod biarticulated (except in *Stenotanais*) (character 97, state 2) and shorter than endopod article 1 (except in *Stenotanais macrodactylus* Larsen, 2005) (character 100, state 1). Marsupium formed from four pairs of oostegites (character 73, state 0). **Male**. Preparatory male with five antennule articles. Pleopods present. Adult male probably of the swimming-type (character 101, state 1) although this has never been conclusively demonstrated by molecular studies.

Genera included. *Akanthophoreus*; *Chauliopleona*; *Mimicarhaphura*; *Parakanthophoreus* n. gen.; *Paraleptognathia*; *Stenotanais*; *Tumidochelia*.

Remarks. The Akanthophoreinae, as a subfamily under Anarthruridae, was erected by Sieg (1986) who also designated *Akanthophoreus* as the type genus. Sieg (1986) transferred to this genus a number of leptognathiid species, including the type species of *Akanthophoreus*, *A. gracilis* (Krøyer, 1842).

The synonymization of *Akanthophoreus* with *Paraleptognathia* by Guerrero-Kommritz (2004) is a controversial issue and is not accepted by Bird (2007) or WoRMS (accessed on 15 Feb 2014). Sticking points include the extensive surface ornamentation on the carpus, propodus, fixed finger and proximal denticulations on the fixed finger found on both *P. typica* Kudinova-Pasternak, 1981 (type species of *Paraleptognathia*) and *P. bacescui* Kudinova-Pasternak, 1985, and the apparent presence of three ventral setae on the cheliped fixed finger of *P. typica*.

These characters are not found in the other species synonymized with *Paraleptognathia* by Guerrero-Kommritz (2004). While the cheliped ornamentation presents few problems (although also found in other unrelated genera), the fixed finger proximal denticulations, attributed much weight by Bird (2007), is not clear and the illustrations by Kudinova-Pasternak (1981) are not up to a modern standard.

While we believe that both Guerrero-Kommritz (2004) and Bird (2007) present convincing arguments for their respective (and contrary) point of views, it is not possible to verify the crucial characters (the fixed finger proximal denticulations and number of ventral setae) as the types of Kudinova-Pasternak are destroyed. We therefore here accept the validity of *Paraleptognathia* for those species with cheliped setulation (ornamentation) on the carpus, propodus, and fixed finger, at least until fresh material can be examined (of *P. typica* and *P. bacescui*). However, we also accept the validity of *Akanthophoreus* regarding the species with telson spurs (*A. gracilis*; *A. lispopygmos* Błażewicz-Paszkowycz *et al*., 2013; *A. phillipsi* (Sieg & Dojiri, 1991); *A. undulatus* Bird, 2007). The remaining '*Akanthophoreus'* species synonymized with *Paraleptognathia* by Guerrero-Kommritz (2004) or those described hereafter create a problem. It seems prudent here to resolve this by raising a new genus (see below) for the species that lack both the extensive surface ornamentation on the carpus, propodus, and fixed finger, and the proximal fixed finger denticulations (characters thus becoming diagnostic for *Paraleptognathia*), as well as those without pleotelson spurs (this character then becoming diagnostic for *Akanthophoreus*).

The restricted phylogenetic analysis performed during this study (Figure 39) supports the monophyletic nature of the family with a Bremer value of 11. The new family diagnosis given here seems, by tanaidacean standards, very stable and clearly separates Akanthophoreidae from Sieg´s (1986) parent family Anarthruridae (although this was a much more inclusive taxon before or since Sieg's revision). It is possible that some species currently assigned to the poorly defined family Leptognathiidae Sieg, 1976 in the genus *Biarticulata* Larsen & Shimomura, 2007 (e.g. *B. elegans* Kudinova-Pasternak, 1965; *B. parelegans* Kudinova-Pasternak, 1970; *B. greveae* Kudinova-Pasternak, 1976; *B. parabranchiata* Kudinova-Pasternak, 1977(*); *B. mironovi* Kudinova-Pasternak, 1981) should be transferred to Akanthophoreidae. However, these species are too incompletely described for key characters to be assigned with confidence. *Gejavis* is another closely related genus but differs from the new diagnosis by: the small maxilla; the maxilliped palp having outer seta on article 1 but not on article 2; the pereopods 4–6 propodus and dactylus lacking the setule/spinules. The maxilliped palp seta on article 1 illustrated by Błażewicz-Paszkowycz & Bamber (2012: 208, fig.139H, 210) is, however, probably a mistake. This genus must be considered *incertae sedis* until a more comprehensive phylogenetic analysis can be performed.

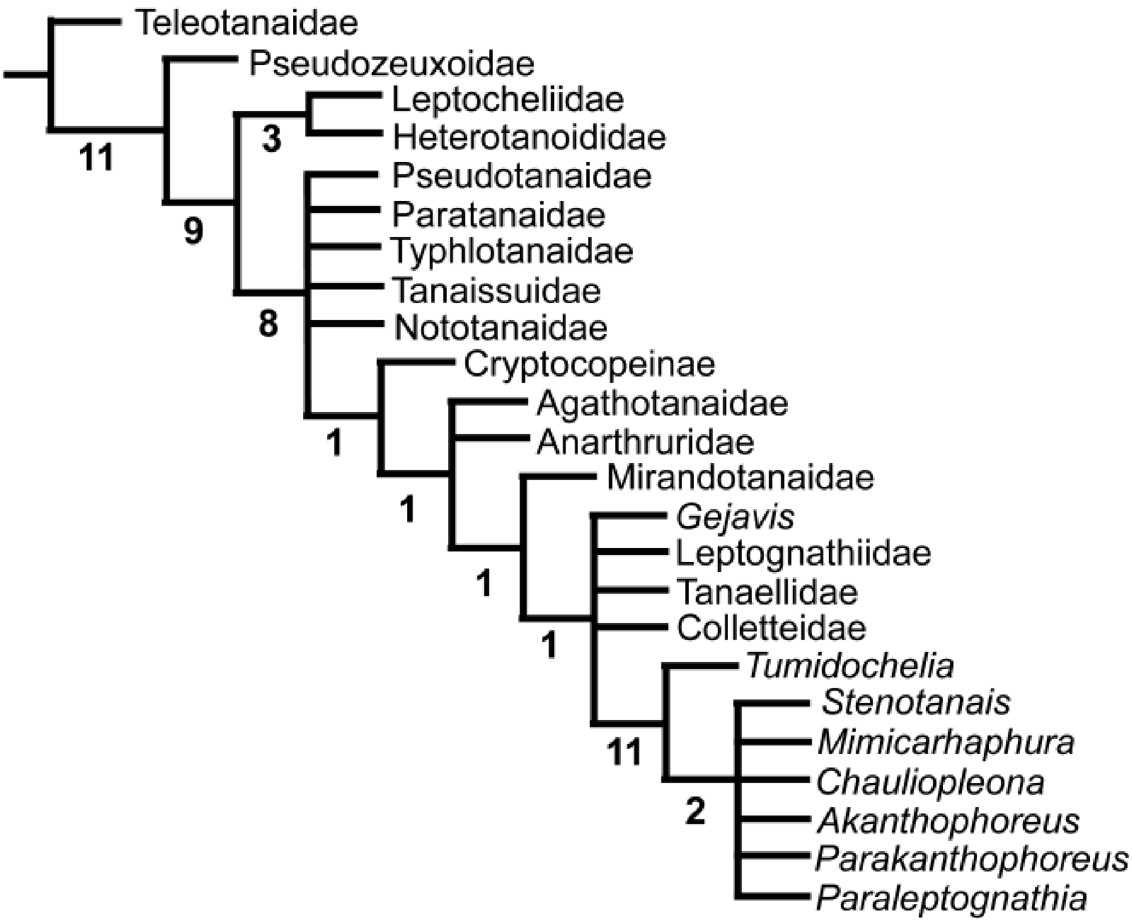


Figure 39. Strict consensus tree (tree length 255) of a restricted phylogenetic analysis of the Akanthophoreidae. Bremer support values given at nodes.

Key to the genera of Akanthophoreidae

1. Pleonite 5 with posteriorly directed ventral spur..............................*Chauliopleona*

\- Pleonite 5 without posteriorly directed ventral spur...2

2. Pleotelson with lateral spurs..*Akanthophoreus*

- Pleotelson without lateral spurs..3

3. Uropod basal article with accessory spur…......................................*Tumidochelia*

- Uropod basal article without accessory spur...4

4. Uropod endopod article 1 with..*Mimicarhaphura*

- Uropod endopod article 1 without spur...5

5. Cheliped carpus, propodus, and fixed finger with extensive surface ornamentation; fixed finger incisive margin with proximal denticulations..*Paraleptognathia*

- Cheliped carpus, propodus, and fixed finger without extensive surface ornamentation; fixed finger incisive margin without proximal denticulations............6

6. Pereopods 1–3 basis thicker than pereopod 4–6 basis......................*Stenotanais*

- Pereopods 1–3 basis thinner than- or of same width as pereopod 4–6 ....*Parakanthophoreus* n. gen.

Genus *Akanthophoreus* Sieg, 1986

Type-species. *Akanthophoreus gracilis* (Krøyer, 1842)

Amended diagnosis. Pleonite 5 without ventral spur. Pleotelson with lateral spurs. Chelipeds with weak or shallow carpal shield; carpus and propodus without ornamentation; fixed finger incisive margin without proximal denticulations; dactylus always with dorsal denticulation. Uropod basal article without accessory spur; endopod article 1 without spur.

Species included. *Akanthophoreus gracilis*; *A. lispopygmos*; *A. phillipsi*; *A. undulatus*.

Genus *Chauliopleona* Dojiri & Sieg 1997

Type-species. *Chauliopleona* dentata Dojiri & Sieg, 1997

Diagnosis. See Larsen & Shimomura (2007)

Generic Remarks. The genus *Chauliopleona* was only described 17 years ago (Dojiri & Sieg 1997), but the number of species has increased rapidly since then, mainly due to the revision by Guerrero-Kommritz (2005). While a common genus, *Chauliopleona* is systematically troublesome and it has been assigned both to the family Anarthruridae (Sieg & Dojiri 1991; Dojiri & Sieg 1997; Guerrero-Kommritz 2005) and the family Akanthophoreidae (Błażewicz-Paszkowycz & Bamber 2012) or considered *incertae sedis* in a phylogenetic analysis by Larsen & Wilson (2002). The posteriorly-directed ventral apophysis on pleonite 5 has previously been recorded as very variable between species, both in relative length and angle (Guerrero-Kommritz 2005). We can confirm this observation here but also found intraspecific variation that seems to be dependent on a specimen's size.

Chauliopleona is now considered a widespread genus, with an impressively wide bathymetric distribution range, extending from shallow water at 23 m (Larsen & Shimomura 2009), 90–278 m (Dojiri & Sieg 1997; Larsen & Shimomura 2007), to, and particularly in, the deep-sea (Larsen 2005; Guerrero-Kommritz 2005; Bird 2007). Geographically, it has previously been collected in both polar regions (Hansen 1913; Guerrero-Kommritz 2005), the North-east Atlantic (Holdich & Bird 1985), the Angola Basin (Guerrero-Kommritz 2005), the Gulf of Mexico (Larsen 2005), off California (Sieg & Dojiri 1991; Dojiri & Sieg 1997), in Japanese waters (Kudinova-Pasternak 1984; Larsen & Shimomura 2007, 2009), including the Kurile-Kamchatka Trench (Kudinova-Pasternak 1970; Bird 2007), New Zealand (Gordon 2010), and recently also in the mid-Pacific Ocean (Larsen, unpublished data). This genus is likely to be present in all major oceans and the current lack of reports from the Indian Ocean is likely to reflect sampling effort rather than a true picture of the distribution.

Species included. *C. amdrupi* (Hansen, 1913); *C. amftae* Guerrero-Kommritz, 2005; *C. andeepi* sp. nov.; *C. armata* (Hansen, 1913); *C. ciimari* sp. nov.; *C. dentata*; *C. faini* Larsen, 2005; *C. hansknechti* Larsen & Shimomura, 2007; *C. hastata* (Hansen, 1913); *C. nickeli* Guerrero-Kommritz, 2005; *C. paradoxa* Guerrero-Kommritz, 2005; *C. sinusa* Larsen & Shimomura, 2009.

Chauliopleona nickeli Guerrero-Kommritz 2005

Material examined. One non-ovigerous female, ANDEEP III, DZMB-HH 3184, station 78, 71°09.52'S, 014°00.76'W (eastern part of the Weddell Sea), 2182 meters, 22 Feb 2005, EBS-epi. One non-ovigerous female, ANDEEP-SYSTCO, DZMB-HH 1541, station 39, 64°28.77'S, 002°52.69'E, 2151.7 meters, 14 March 2002, EBSepi.

Remarks. The new records extend the distribution range of this Antarctic species by about 10 degrees of both latitude and longitude, and the bathymetric range by around 100 m.

Chauliopleona ciimari **n. sp.**

(Figures 40–42)

Material examined. Holotype: female, ANDEEP-SYSTCO, DZMB-HH 1550, station 85, 52°01.54'S, 000°00.22'E (northwest of Buvetøya Island), 2987.4 meters, 27 Jan 2008, EBS-epi (ZMH K-44132).

Paratypes: One female, same locality, dissected (ZMH K-44133). Two non-ovigerous females, ANDEEP-SYSTCO, DZMBHH 1360, station 24, 52°01.98'S, 00°01.12'W, 2997.9 meters, 06 Dec 2007, EBS-epi (processed for DNA analysis).

Diagnosis. **Female**. Cephalothorax longer than pereonites 1 and 2 combined. Pereonites with curved lateral margins. Antennule article 1 as long as rest of antennule. Antenna article 3 with long (0.4 times as long as article 4) dorsal seta; article 4 without fusion line. Maxilliped basis with long setae (almost as long as palp); palp article 2 with spiniform serrated seta and long seta (almost reaching end of palp) on outer margin. Cheliped merus without ventral process, carpal shield shallow but with anterior acute angle, propodus and dactylus without crenulations. Pereopod 1 with carpus bearing ventrodistal row of spinules.

Etymology. Named after the authors' institution CIIMAR (Centro Interdisciplinar de Investigação Marinha e Ambiental).

Description. Female. Body from holotype and paratype, appendages from dissected paratype.

Body (Figure 40A, B) elongate, 2.15 mm long, about nine times as long as wide. Cephalothorax longer than pereonites 1 and 2 combined. Pereonites all wider than long. Pleon short (including pleotelson shorter than 20% of total body length). All pleonites subequal in length and width (pleopods not drawn). Pleonite 5 posterior-directed spur reaching midlength of pleotelson. Pleotelson (Figure

40C) longer than two last pleonites combined, widening medially, apex rounded, with three pairs of terminal setae.

Antennule (Figure 41A) shorter than cephalothorax. Article 1 as long as other articles combined, with numerous small simple dorsoproximal setae, two setulose medial setae, and one simple and one setulose distal setae. Article 2 less than half as long as article 1, with two simple distal setae and three setulose subdistal setae. Article 3 shorter than article 2, with two simple distal setae. Article 4 longer than article 3, with two long distal setae. Terminal cap-like article partly fused with article 4 and represented as a dorsal protrusion, with five simple setae and one aesthetasc.

Antenna (Figure 41B) 0.75 times as long as antennule. Article 1 as long as article 3, naked. Article 2 slightly longer than article 5, with numerous proximal setules and one dorsodistal seta. Article 3 shorter than article 2, with one long (0.4 times as long as article 4) dorsodistal seta. Article 4 longer than other articles, without fusion line, with one medial and two setulose distal setae and three simple distal setae of which two are longer than article 5. Article 5 less than half as long as article 4, with one short and two long distal setae. Article 6 minute, with six simple distal setae of which one is tiny.

Mouthparts (Figure 41C–J). Labrum (Figure 41C) rather pointed, with smooth apex, with ventral setulose posteriorlydirected projection. Mandibles (Figure 41D, E) molar process tapering distally, longer than incisor, with small distal spines. Right mandible (Figure 41D) incisor with four irregular denticles. Left mandible (Figure 41E) lacinia mobilis blunt, shorter than incisor; incisor with three denticles. Labium (Figure 41F) with setulated outer corners and inner seta. Maxillule (Figure 41G) endite with nine apical spiniform setae of which at least two are serrated, shaft with several small setules on both margins; palp shorter than endite with two long distal setae. Maxilla (Figure 41H) remarkably large (almost as large as mandible), widest at base, with evenly spaced setules. Maxilliped (Figure 41I) basis with long lateral seta near palp attachment; endites narrower than basis, not fused, each with inner, unarticulated denticles and one outer robust and one inner simple setae. Palp article 1 naked; article 2 with one long (as long as palp) seta on outer margin, three thick, long setae on inner margin (of which one is specialized); article 3 with one simple and three thick setae, thick long setae on inner margin; article 4 only half as wide as article 3, with four inner thick setae and one subdistal outer simple seta. Epignath (Figure 41J) slender and naked.

Cheliped (Figure 41D) with basis unequally divided by long prominent sclerite, marginally shorter than carpus. Merus triangular, with one ventromedial seta. Carpus as long as propodus (including fixed finger), widest proximally, with two ventromedial setae and one small dorsal seta at each end, carpal shield relatively shallow/weak but with anterior acute angle. Propodus slender (l/w ratio 2.2), dorsal crest low and with no crenulations, with simple seta at dactylus insertion and diagonal row of five robust inner setae, of which one is pinnate. Fixed finger with two ventral setae and three on inner margin, inner margin with four blunt denticles. Dactylus as long as fixed finger, without crenulations on dorsal margin, with proximal simple seta.

Pereopod 1 (Figure 42A) coxa with one simple seta. Basis marginally longer than three succeeding articles combined (l/w ratio 2.6), with one simple and one setulose dorsomedial setae. Ischium with one ventral seta. Merus marginally shorter than carpus, widening distally, with one long, bayonet seta and one simple distal seta. Carpus more than half as long as propodus, with one long (almost as long as propodus), spiniform distal seta on each margin and distal small spines. Propodus more than half as long as basis, ventral margin with numerous small spines, one spiniform ventrodistal seta, one dorsomedial simple seta and dorsodistal spines. Dactylus broken but with one long proximal simple seta and small spines.

Pereopod 2 (Figure 42B) as pereopod 1 except: basis with two dorsomedial simple, and one setulose setae; carpus with one small simple and three spiniform distal setae. Dactylus and unguis combined shorter than propodus.

Pereopod 3 (Figure 42C) as pereopod 2 except: basis with one setulose dorsomedial seta. Propodus with three small dorsodistal spines. Dactylus longer than unguis.

Pereopod 4 (Figure 42D) coxa fused to body. Basis more slender than those of pereopods 1–3 (l/w ratio 3.3), with two setulose dorsomedial setae. Ischium with two setae. Merus with two spiniform setae (half as long as carpus). Carpus with one “bone-shaped” dorsodistal seta and three spiniform distal setae. Propodus with two spiniform ventrodistal setae, one simple seta and one spine dorsodistally. Dactylus shorter than propodus, with one simple proximal seta and

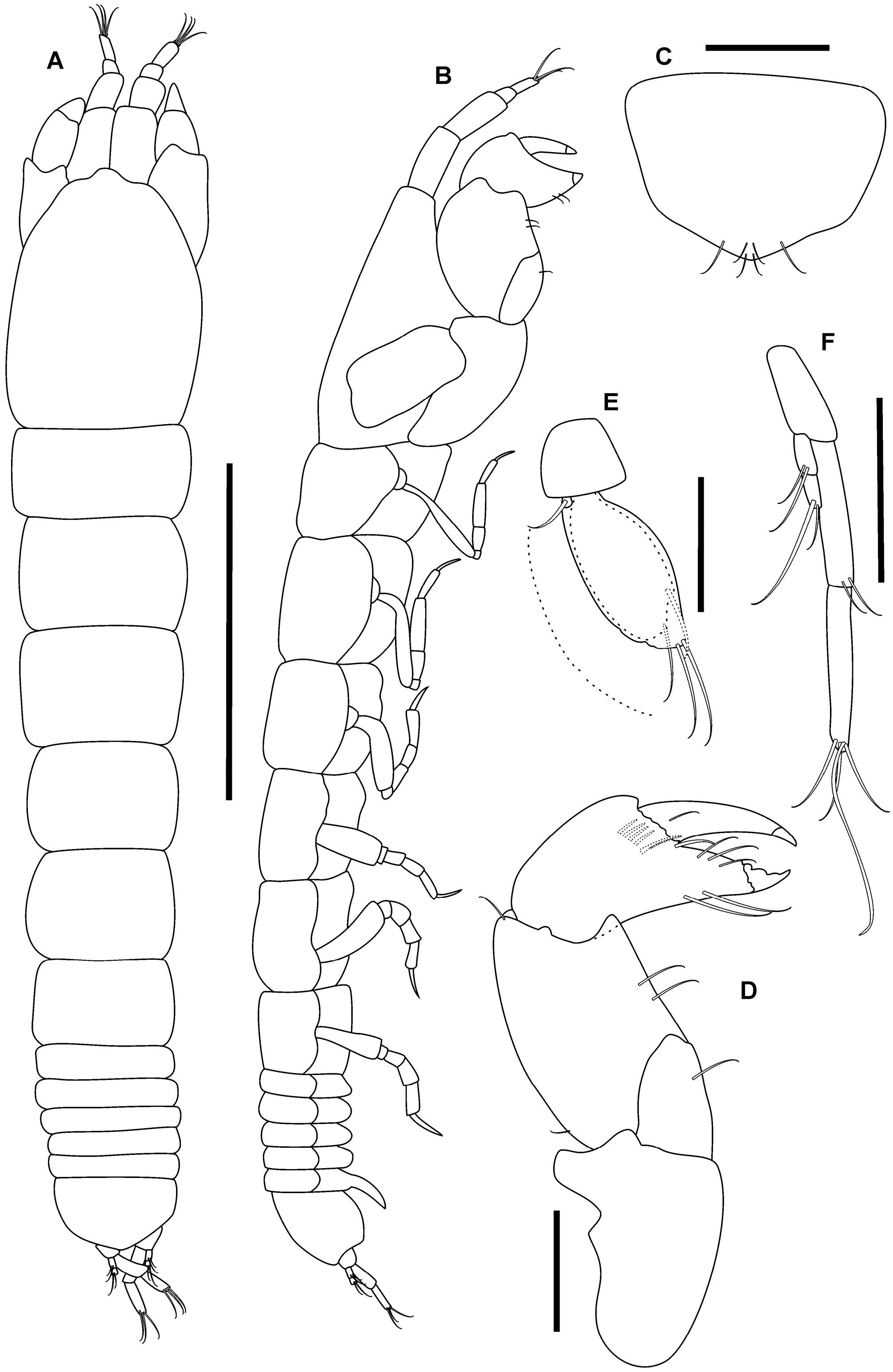


Figure 40. *Chauliopleona ciimari* n. sp., female. (A), holotype, dorsal view; (B), paratype, lateral view scale bar 1.0 mm; (C), pleotelson; (D), cheliped; (E), pleopod; (F), uropod. Scale bar: 0.5 mm.

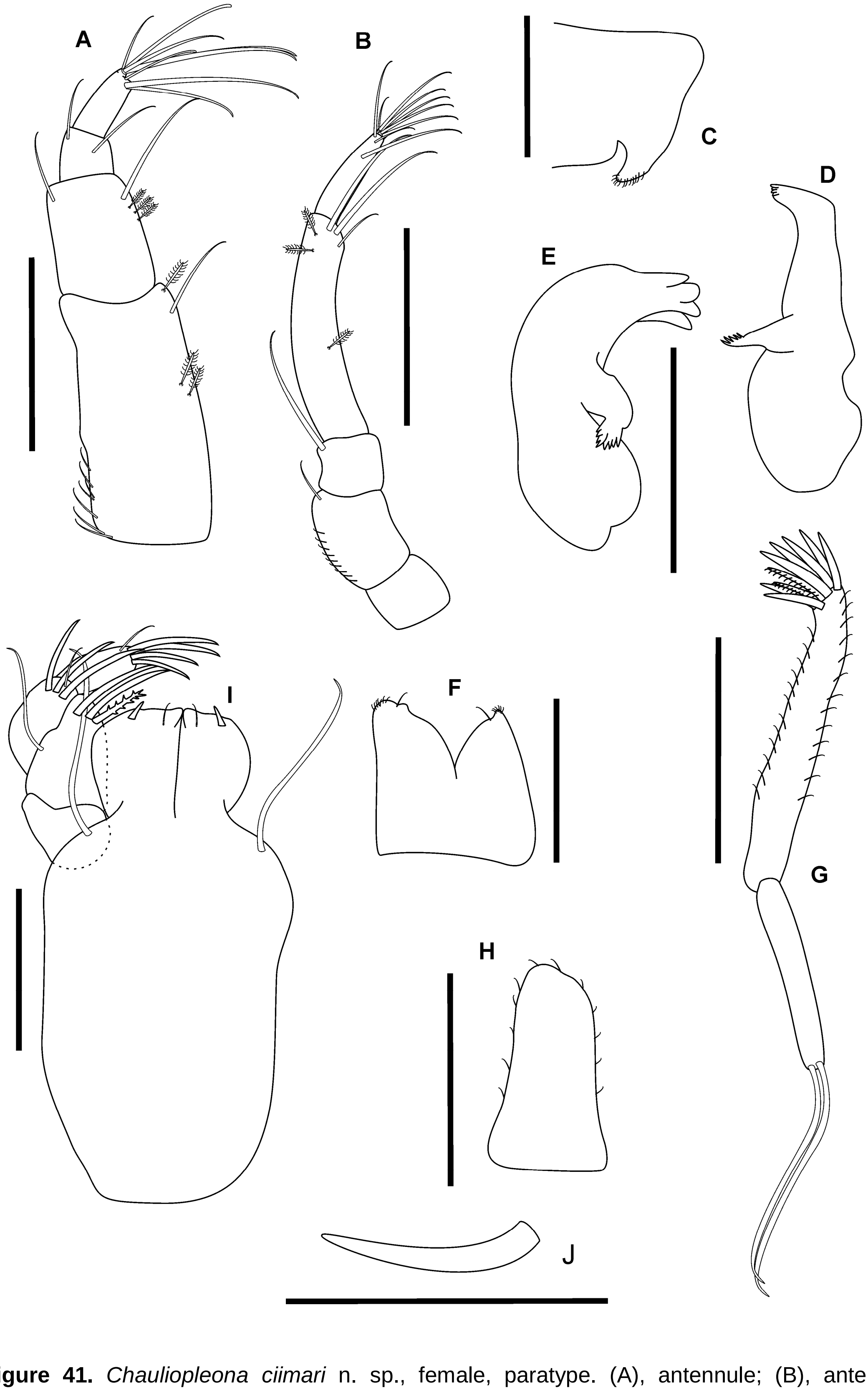


Figure 41. *Chauliopleona ciimari* n. sp., female, paratype. (A), antennule; (B), antenna; (C), labrum; (D), right mandible; (E), left mandible; (F), labium; (G), maxillule; (H), maxilla; (I), maxilliped; (J), epignath. Scale bar: 0.1 mm.

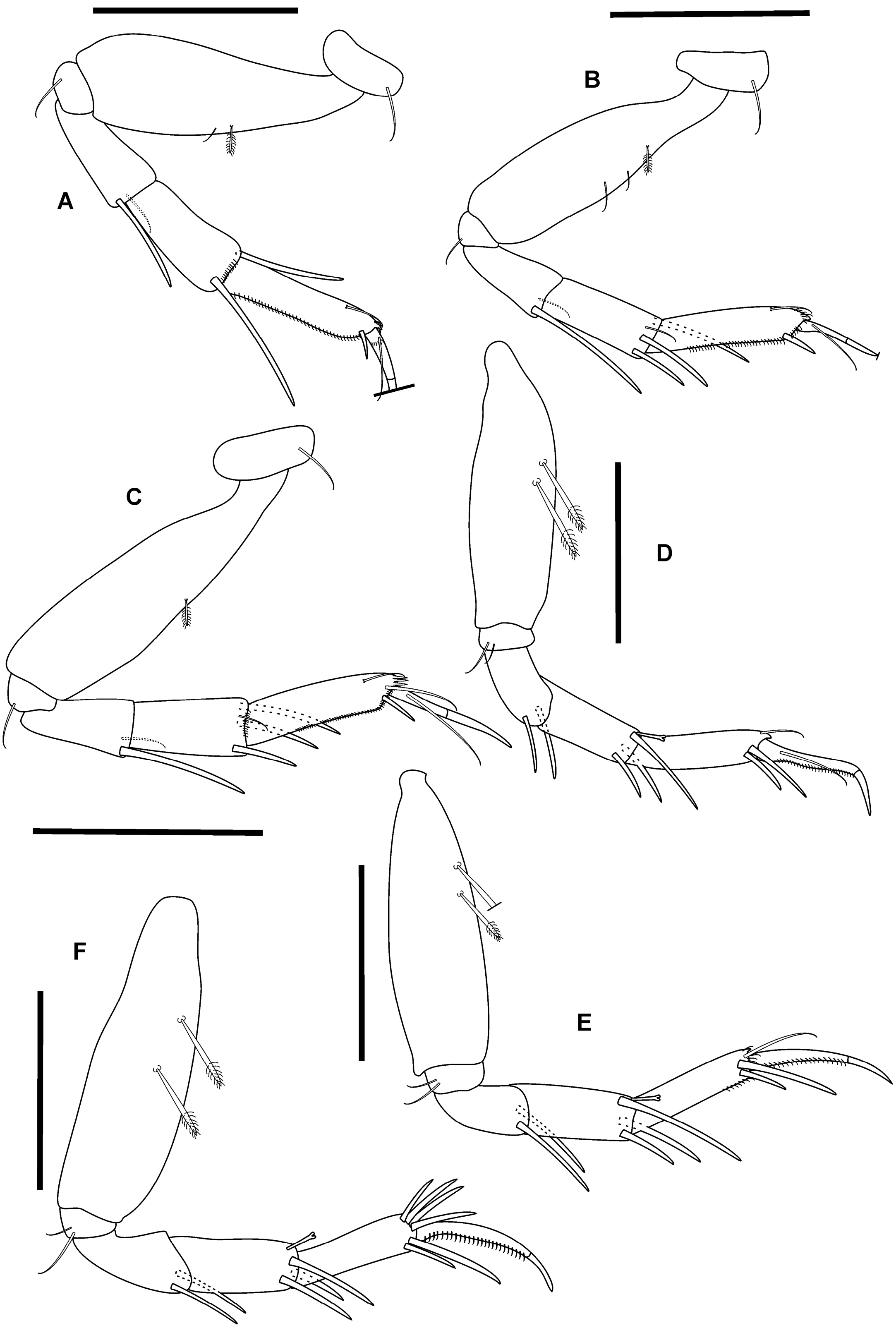


Figure 42. *Chauliopleona ciimari* n. sp., female, paratype. (A), pereopod 1; (B), pereopod 2; (C), pereopod 3; (D), Pereopod 4; (E), pereopod 5; (F), pereopod 6. Scale bar: 0.5 mm.

two rows of small ventral spines separated by a groove; unguis clearly demarcated, less than half as long as dactylus.

Pereopod 5 (Figure 42E) as pereopod 4 except: propodus with several small ventral spinules.

Pereopod 6 (Figure 42F) as pereopod 5 except: propodus with four dorsodistal spiniform setae and two dorsodistal spines (not illustrated).

Pleopods (Figure 40E) subequal. Endopod with one outer and 13 apparently simple inner setae. Exopod with basal seta arising from an incompletely fused rudimentary article and separated from other setae by a gap, with 13 apparently simple setae of which the most distal is shorter and thicker than the adjacent ones.

Uropod (Figure 40F) longer than pleotelson. Basal article longer than exopod, naked. Endopod with two subequal [length] articles; article 1 with two simple distal setae; article 2 with one long subdistal seta and three simple distal setae. Exopod with two articles, half as long as first endopod article; article 1 with two distal setae; article 2 with two long unequal distal setae.

Remarks. This species keys out to *Chauliopleona armata* using Guerrero-Kommritz's key from (2005) but can be separated from this North Atlantic species and subsequently described species (*C. faini*, *C. hansknechti*, and *C. sinusa*) by the carpal shield having its anterior acute angle.

Chauliopleona andeepi **n. sp.**

(Figures 43–45)

Material examined. Holotype: non-ovigerous female, ANDEEP I, DZMB-HH 10379, station 42, 59°40.29'S, 57°35.43'W (northwest of King George Island), 3683 meters, 27 Jan 2002, EBS-epi. (Zmh k-44134).

Paratypes: one non-ovigerous female, same location, dissected (ZMH K-44135). Three non-ovigerous females, ANDEEP I, DZMB-HH 10380, station 42, 59°40.29'S, 57°35.43'W, 3683 meters, 27 Jan 2002, EBS-epi (ZMH K-44136). One non-ovigerous female, ANDEEP I, DZMB-HH 10381, station 43, 60°27.12'S, 56°05.10'W, 3961 meters, 04 Feb 2002, EBS-epi (ZMH K-44137). One non-ovigerous female (broken), ANDEEP I, DZMB-HH 10382, station 46, no locality data given, 2926 meters, 28 Jan 2002, ATC.

Diagnosis. **Female**. Cephalothorax shorter than pereonites 1 and 2 combined. Pereonites with convex lateral margins. Antennular article 1 shorter than rest of antennule. Antenna article 3 with long (0.4 times as long as article 4) dorsal seta, article 4 with fusion line. Maxilliped basis with long setae (almost as long as palp); palp article 2 with robust serrated inner seta and one long (longer than rest of palp) seta on outer margin. Cheliped merus without ventral process, carpal shield large but without ventral acute-angled process; propodus and dactylus without dorsal crenulations. Pereopods 1–3 basis wider than those of pereopods 4–6.
Etymology. Named after the ANDEEP expeditions.

Description. Female. Body from holotype, appendages from dissected paratype.

Body (Figure 43A, B) elongate, 1.8 mm long, more than ten times as long as wide. Cephalothorax shorter than pereonites 1 and 2 combined. Pereonites 1 and 6 wider than long; pereonites 2–4 longer than wide; pereonite 5 square. Pleon short (length including pleotelson about 22% of total body length). All pleonites subequal in length and width. Pleonite 5 posteriorly-directed spine on ventral margin reaching midlength of pleotelson. Pleotelson (Figure 43F) as long as two last pleonites combined, widening medially, apex rounded, with three simple and one setulated, pairs of terminal setae.

Antennule (Figure 44A) shorter than cephalothorax. Article 1 shorter than other articles combined, without dorsoproximal setae, with one setulose medial seta, and four simple and one setulose distal-subdistal setae. Article 2 more than half as long as article 1, with two setulose, and four simple distal setae of which two are longer than article 3. Article 3 less than half as long as article 2, with three simple and one setulose, distal setae. Article 4 marginally shorter than article 2, with partly fused terminal minute cap-like article, with four simple distal setae and a broken structure that is probably an aesthetasc.

Antenna (Figure 44B) 0.75 times as long as antennule. Article 1 broken. Article 2 broken, with numerous dorsal setules and one dorsodistal seta. Article 3 shorter than article 5, with one long (0.4 times as long as article 4) dorsodistal seta. Article 4 longer than other articles, with fusion line, with one medial, one subdistal, and one distal setulose setae and three simple distal setae. Article 5 less than half as long as article 4, with two long distal setae. Article 6 minute, with five simple distal setae.

Mouthparts (Figure 44C–I). Labrum (Figure 44C) with setulose apex and ventral smooth projection. Mandibles (Figure 44D–E) molar process tapering distally, longer than incisor, with small distal spines. Right mandible (Figure 44D) incisor with three denticles. Left mandible (Figure 44E) lacinia mobilis large and with several denticles, shorter than incisor; incisor bifurcate and with two additional outer denticles. Labium (Figure 44F) lobes with setulose apex. Maxillule (Figure 44G) endite with eight apical serrated spiniform setae, shaft with several small setules on both margins; palp shorter than endite with two long distal setae (not drawn). Maxilla (Figure 44G) remarkably large (almost as large as mandible), widest at base, with numerous evenly spaced small setules. Maxilliped (Figure 44H) basis with long (almost as long as palp) lateral seta near palp insertion; endites narrower than basis, separate, each with unarticulated inner denticles and outer seta. Palp article 1 naked; article 2 with one long (longer than rest of palp) simple seta on outer margin, two thick and one robust serrated setae (not as strong as in the previous species) on inner margin; article 3 with two simple short and two thick longer setae on inner margin; article 4 only half as wide as article 3, with four thick inner and one subdistal outer simple setae. Epignath (Figure 44I) slender and with setulose apex.

Cheliped (Figure 43C) with basis unequally divided by long prominent sclerite (illustrated in Figure 43B), shorter and much thinner than carpus, apparently naked. Merus triangular, with one ventromedial seta. Carpus longer than propodus (including fixed finger), widest distally, with two ventromedial seta and one small dorsal seta at each end, carpal shield huge but not strongly demarcated. Propodus (Figure 43D) l/w ratio 1.5; dorsal crest absent and without crenulations, with dorsodistal small simple seta and larger seta at dactylus insertion, with inner diagonal row of four inner setae. Fixed finger with two ventral setae and three on inner margin, inner margin with two small blunt denticles. Dactylus as long as fixed finger, without dorsal crenulations, naked.

Pereopod 1 (Figure 45A) coxa naked, not illustrated. Basis longer than three succeeding articles combined and wider than that of pereopods 4–6 (l/w ratio 1.9), with one small simple ventrodistal seta. Ischium with one ventral seta.

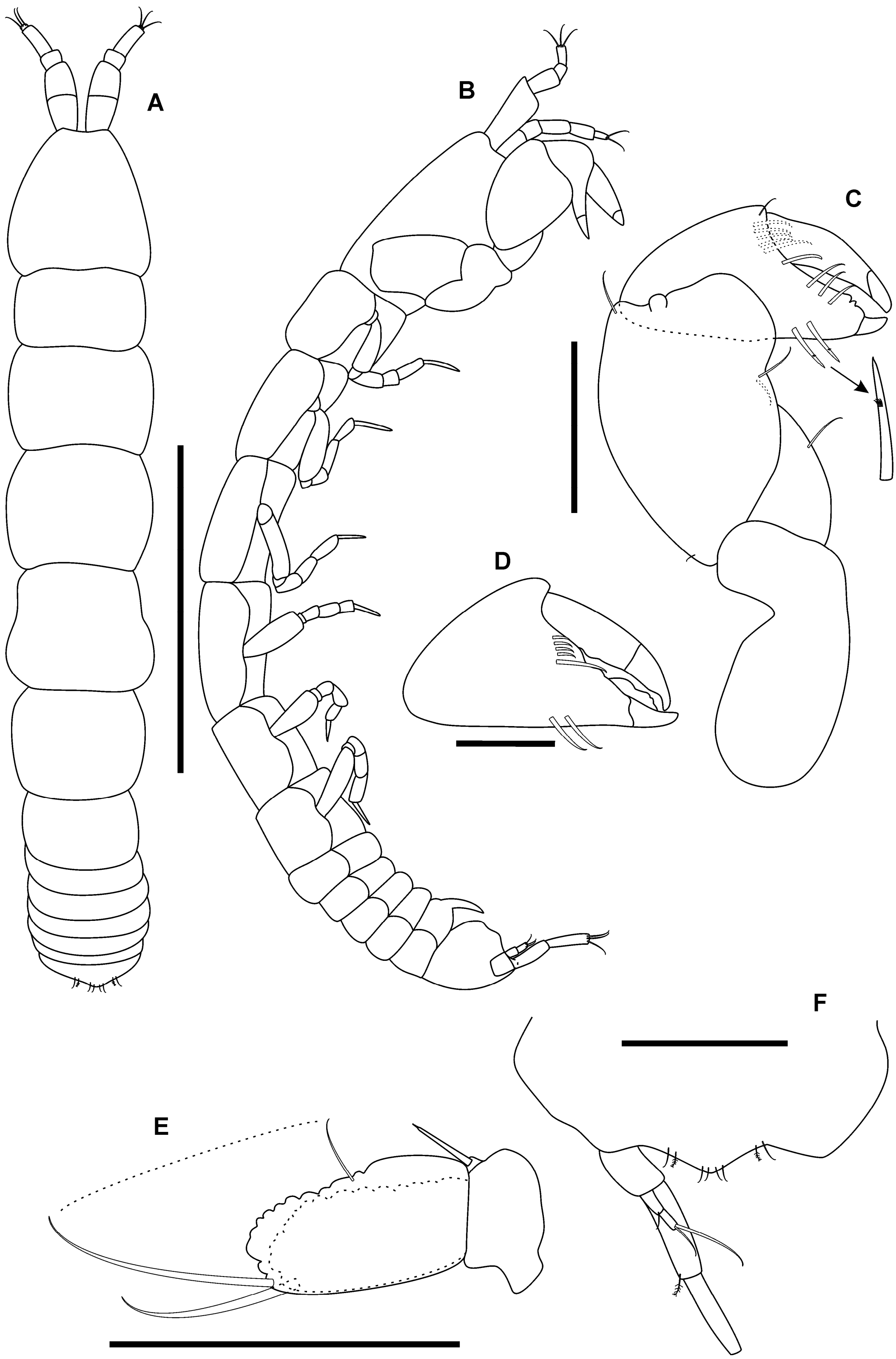


Figure 43. *Chauliopleona andeepi* n. sp., female. (A), holotype, dorsal view; (B), paratype, lateral view; (C), cheliped; (D), same, propodus and dactylus; (E), pleopod; (F), pleotelson and uropod. Scale bars: (A-B), 1.0 mm; (C-F), 0.5 mm.

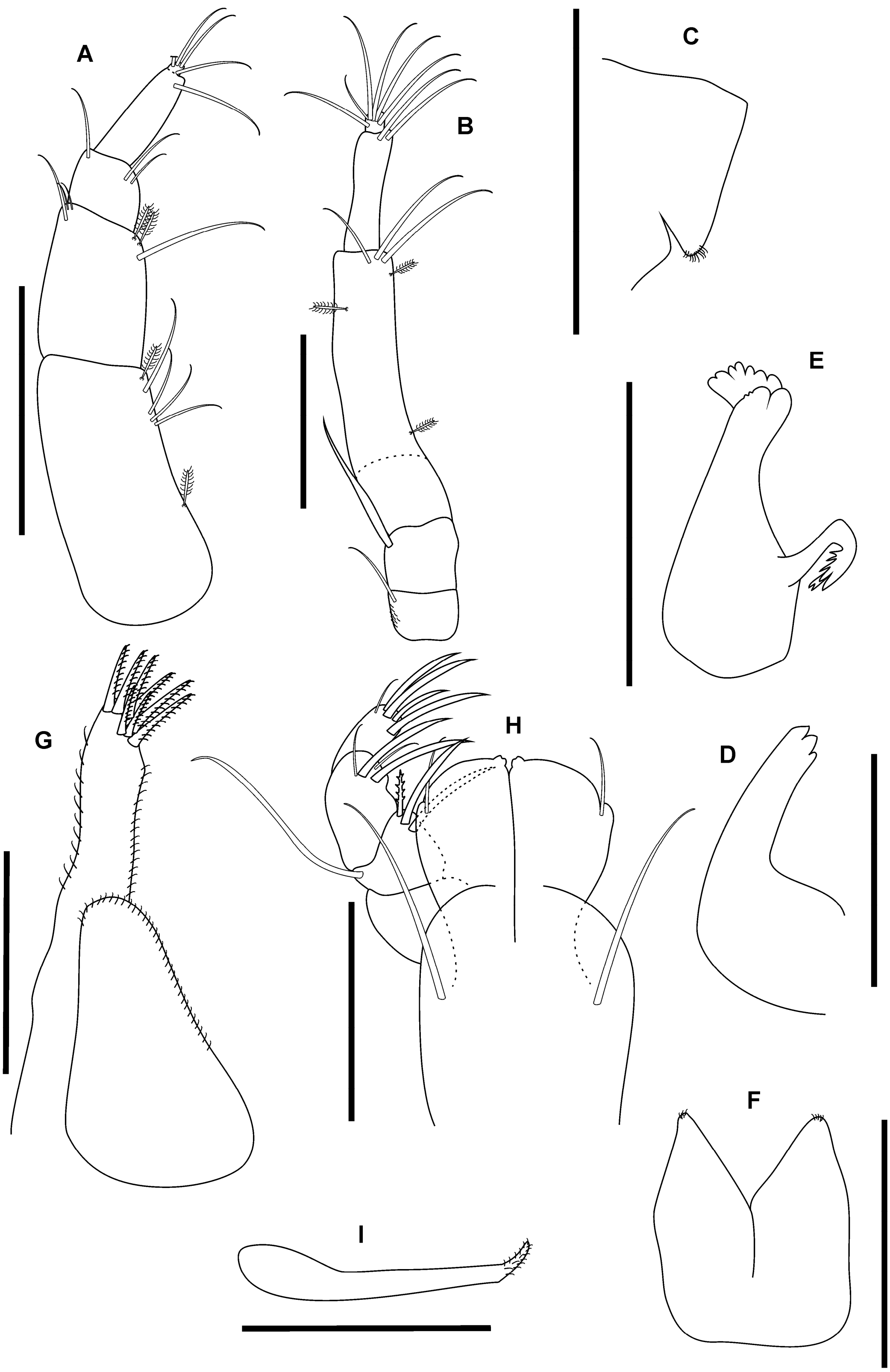


Figure 44. *Chauliopleona andeepi* n. sp., female, paratype. (A), antennule; (B), antenna; (C), labrum; (D), right mandible; (E), left mandible; (F), labium; (G), maxillule and maxilla; (H), maxilliped; (I), epignath. Scale bars: 0.1 mm.

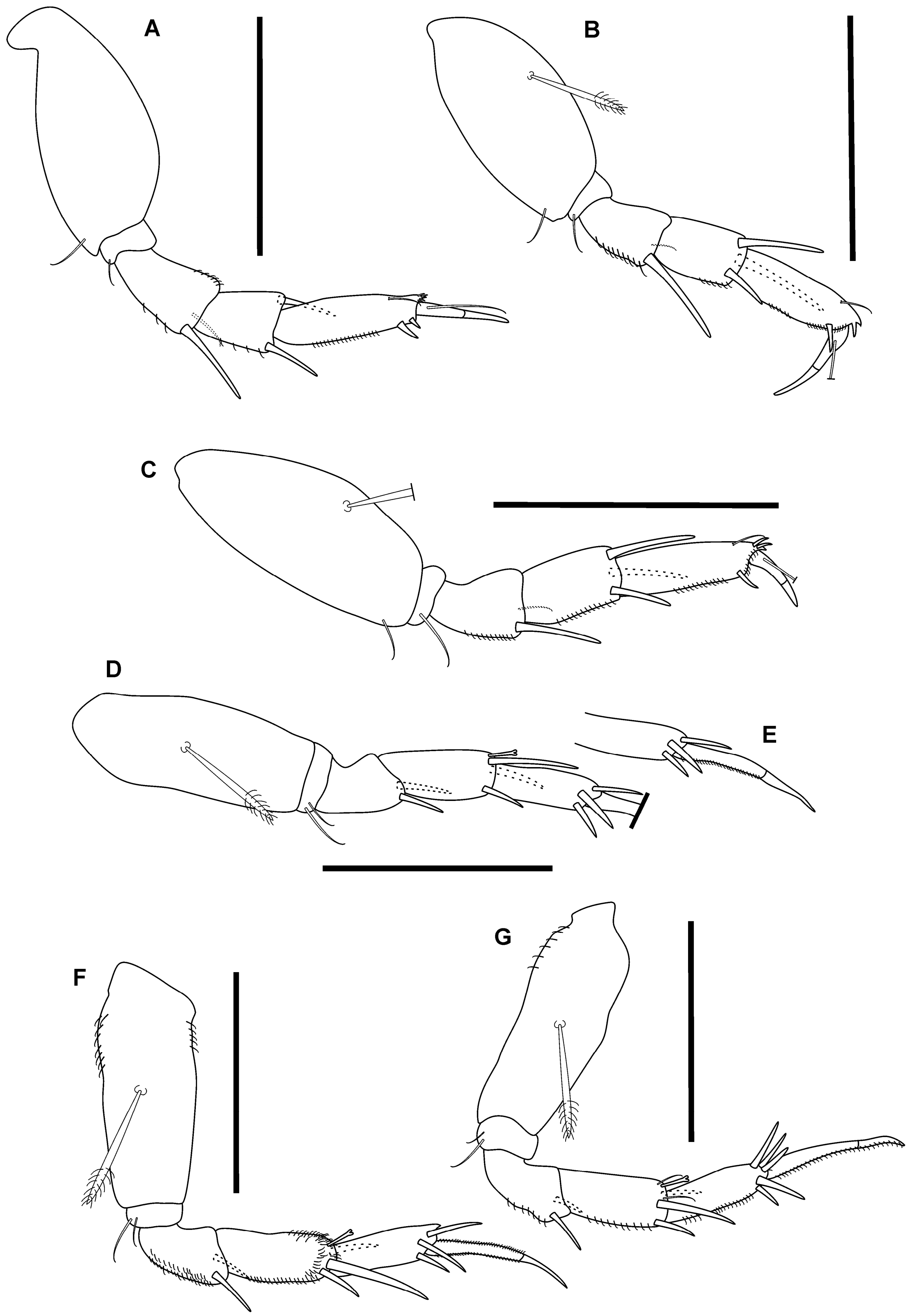


Figure 45. *Chauliopleona andeepi* n. sp., female, paratype. (A), pereopod 1; (B), pereopod 2; (C), pereopod 3; (D), left pereopod 4; (E), right pereopod 4, dactylus; (F), pereopod 5; (G), pereopod 6. Scale bar: 0.5 mm.

Merus marginally shorter than carpus, widening distally, with one long, spiniform seta and one simple seta distally, and both ventral and dorsal setules. Carpus more than half as long as propodus, with one spiniform distal seta on each margin and ventral setules. Propodus more than half as long as basis, ventral margin with numerous small spines, with two spiniform ventrodistal setae and several small dorsodistal spines and dorsal seta. Dactylus and unguis combined about half as long as propodus, with one simple proximal seta.

Pereopod 2 (Figure 45B) as pereopod 1 except: basis with setulose dorsomedial seta. Carpus with three long spiniform distal setae. Propodus with one spiniform ventrodistal seta and two dorsodistal spines.

Pereopod 3 (Figure 45C) as pereopod 2.

Pereopod 4 (Figure 45D, E) coxa fused to body. Basis more slender than those of pereopods 1–3 (l/w ratio 2.6), with long setulated ventroproximal seta. Ischium with two setae. Merus with two spiniform setae. Carpus with three spiniform setae and one "bone-shaped" distal seta. Propodus with two spiniform ventrodistal and one dorsodistal setae and ventral row of small spines. Dactylus (Figure 45E) shorter than propodus, with two rows of small ventral spines; unguis clearly demarcated, less than half as long as dactylus.

Pereopod 5 (Figure 45D) as pereopod 4 except: several ventral and dorsal spinules on basis, merus, and carpus.

Pereopod 6 (Figure 45G) as pereopod 4 except: carpus with two small simple, distal setae. Propodus with two ventrodistal and three dorsodistal spiniform setae.

Pleopods (Figure 43E) subequal. Endopod with one inner and nine outer apparently simple setae. Exopod with basal seta arising from an incompletely fused rudimentary article and separated from other setae by a gap, with nine outer apparently simple setae of which the most distal is shorter and thicker than the adjacent ones.

Uropod (Figure 43F) longer than pleotelson. Basal article as long as exopod, naked. Endopod with two subequal [length] articles; article 1 with one setulated distal seta; article 2 setation lost during dissection. Exopod with two articles, half as long as first endopod article; article 1 with one distal seta; article 2 with one tiny and one long (longer than endopod article) distal setae.

Remarks. This species also keys out to *C. armata* using Guerrero-Kommritz's key (2005) but can be separated from this and most subsequently described species, including *C. cimarii* described above by: the antennule being much more stout and article 1 being shorter than rest of antennule; the cheliped have a much larger carpal shield as well as a much more robust propodus/dactylus. From *C. hastata*, this species can be separated by the much longer antenna article 3.

Genus *Parakanthophoreus* n. gen.

Diagnosis. Pleonite 5 without ventral spur. Pleotelson without lateral spines. Cheliped carpus, propodus, and fixed finger without extensive surface ornamentation; fixed finger without proximal inner denticulations. Uropod basal article without accessory spur; uropod endopod article 1 without spur.

Type-species (by original designation, ICZN article 67b). *Parakanthophoreus greenwichius* sp. nov.

Etymology. The genus name reflects the close and intermediate relationship with both *Paraleptognathia* and *Akanthophoreus*.

Gender. Masculine.

Generic remarks. The new genus is easily separated from its 'parent taxa'- by the lack of pleotelson spurs, lack of cheliped carpal/propodal ornamentation, and lack of proximal fixed finger denticulation.

Species included. See Table 3; mandatory spelling changes have been performed in according with the ICZN article 34.

Parakanthophoreus greenwichius **n. sp.**

(Figures 46–48)

Material examined. Holotype: female, ANDEEP-SYSTCO, DZMB-HH 1360, station 24, 52°01.98' S, 00°01.12'W (southwest of Buvetøya Island), 2997.9 meters, 06 Dec 2007, EBS-epi. (ZMH K-44138).

Paratypes: One female, same locality, dissected (ZMH K-44139). Two non-ovigerous females, ANDEEP-SYSTCO, DZMBHH 10540, station 85, 52°01.54'S, 00°00.22'E, 2987.4 meters, 18 Feb 2002, EBS-epi (ZMH K-44140).

Diagnosis. Female. Cephalothorax shorter than pereonites 1 and 2 combined. Antennule article 1 much shorter than rest of antennule; article 4 with apical setae with wide basis. Maxilliped basis without long setae; endites with robust outer seta. Cheliped merus without ventral process; carpus with huge carpal shield; propodus and dactylus without crenulations; fixed finger with heavy, medially-serrated ventral setae.

Etymology. Named after the Greenwich median (adjectival) as the longitude of the type locality.

Description. **Female**. Body from holotype, appendages from dissected paratype.

Body (Figure 46A, B) elongate, 2.0 mm long, about eight times as long as wide. Cephalothorax shorter than pereonites 1 and 2 combined. Pereonites all wider than long. Pleon short (length including pleotelson about 20% of total body length). All pleonites subequal in length and width. Pleotelson longer than two last pleonites combined, widening medially, apex rounded, with two pairs of terminal setae.

Antennule (Figure 47A) shorter than cephalothorax, with partly fused terminal cap-like article. Article 1 much shorter than other articles combined, very stout (l/w ratio 1.3), with two setulose medial setae, one simple and one setulose distal setae. Article 2 only marginally shorter than article 1, with two simple distal setae and three setulose distal setae. Article 3 only half as long as article 2, apparently naked. Article 4 almost twice as long as article 3, with two long thick, and two short simple distal setae. Terminal cap-like article partly fused with article 4, with two long, thick, and one small simple distal, setae.

Antenna (Figure 47B) 0.75 times as long as antennule. Article 1 broken. Article 2 shorter than article 5, with numerous proximal setules and one dorsodistal simple seta. Article 3 shorter than article 2, with one dorsodistal simple seta. Article 4 longer than other articles, with fusion line, with one subdistal setulose seta at each margin, and three simple distal setae of which two are longer than article 5. Article 5 less than half as long as article 4, with one long distal seta. Article 6, with three distal simple setae.

Mouthparts (Figure 47C–J). Labrum (Figure 47C) with finely setose, rounded apical margin. Mandibles (Figure 47D, E) molar process tapering distally, longer than incisor, with distal spines. Right mandible (Figure 47D) incisor with four weakly defined denticles. Left mandible (Figure 47E) lacinia mobilis blunt, as long as incisor; incisor with three weakly defined denticles. Labium (Figure 47F) consisting of one pair of weakly setose lobes, with lateral extensions (possibly a rudiment of a second pair of lobes). Maxillule (Figure 47G) endite with seven apical spiniform setae, which one is serrated, shaft with several small setules on outer margins; palp broken. Maxilla (Figure 47H) large (almost as large as mandible), widest at base, with evenly spaced setules. Maxilliped (Figure 47I) basis without setae; endites narrower than basis, not fused, each with inner (apparently articulated) denticles and outer robust seta and outer depression with small spines/setules. Palp article 1 naked; article 2 with one simple seta on outer margin, one serrated, and two thick setae on inner margin; article 3 with two long thick and two short thin inner setae; article 4 only half times as wide as article 3, with four long, thick inner and two subdistal thinner outer simple setae. Epignath (Figure 47J) slender and naked.

Cheliped (Figure 46C) with basis unequally divided by long, prominent sclerite, shorter than carpus, with one dorsodistal simple setae. Merus triangular, with one ventromedial seta. Carpus as long as propodus (including fixed finger), widest distally, with two ventromedial seta and one small dorsal seta at each end, carpal shield prominent. Propodus robust (l/w ratio 1.7), dorsal crest low and without crenulations, with simple seta at dactylus insertion but apparently without row of inner setae (possibly an artefact). Fixed finger with two very thick, weakly serrated ventral setae and three thick, simple setae on inner margin, inner margin heavily chitinized but with only two gently curved denticles. Dactylus robust, as long as fixed finger, without crenulations or setae.

Pereopod 1 (Figure 48A) coxa with one simple seta. Basis longer than three succeeding articles combined and wider than that of pereopods 4–6 (l/w ratio 2.3), naked. Ischium with one ventral seta. Merus as long as carpus, widening distally, with one long, spiniform seta and one simple seta ventrodistally. Carpus 0.65 times as long as propodus, with two long, spiniform

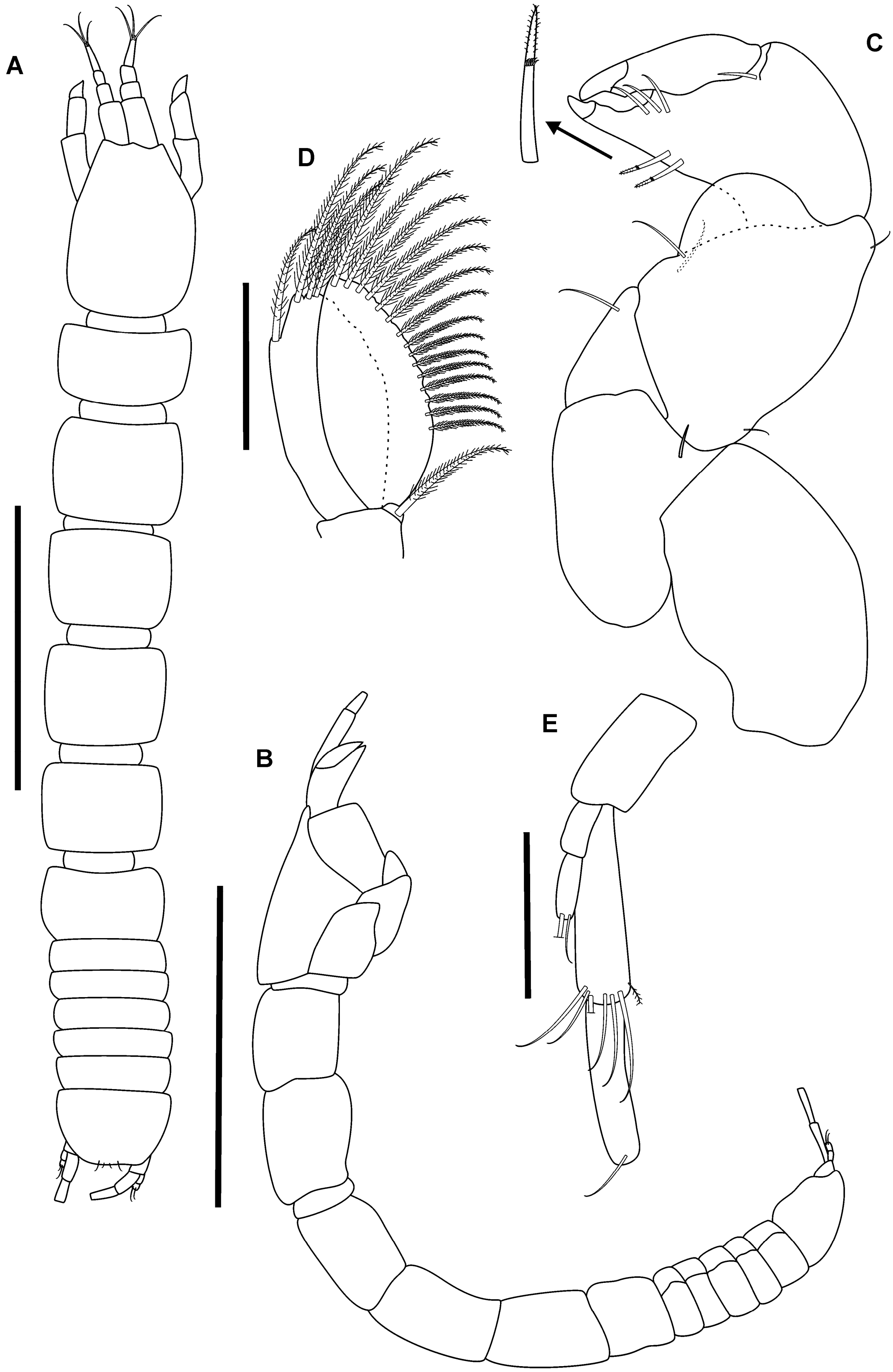


Figure 46. *Parakanthophoreus greenwichius* n. sp., female. (A), holotype, dorsal view; (B), paratype, lateral view; (C), cheliped; (D), pleopod; (E), uropod. Scale bars: (A-B), 1.0 mm; (C-E), 0.5 mm.

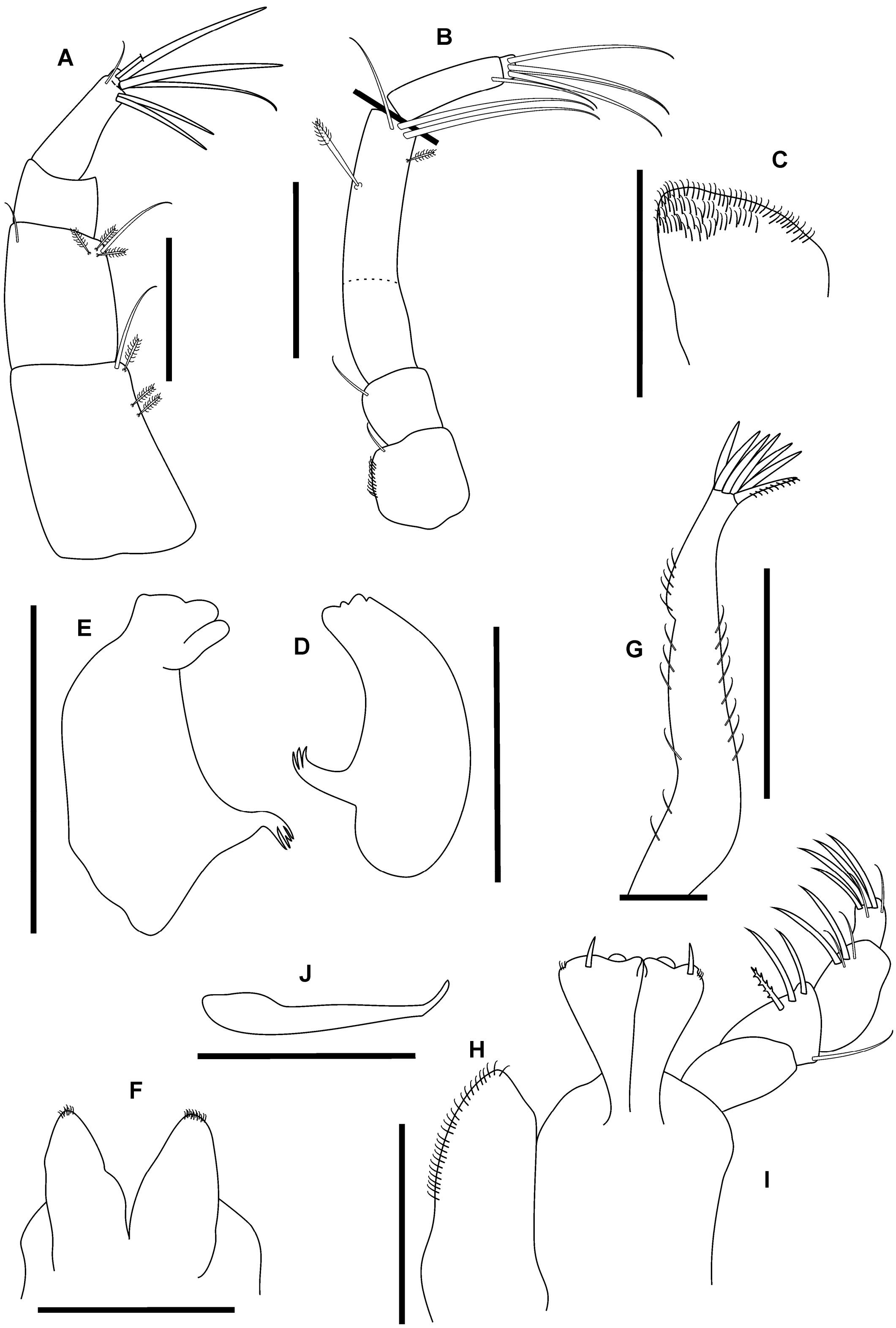


Figure 47. *Parakanthophoreus greenwichius* n. sp., female, paratype. (A), antennule; (B), antenna; (C), labrum; (D), right mandible; (E), left mandible; (F), labium; (G), maxillule; (H), maxilla; (I), maxilliped; (J), epignath. Scale bars: 0.1 mm.

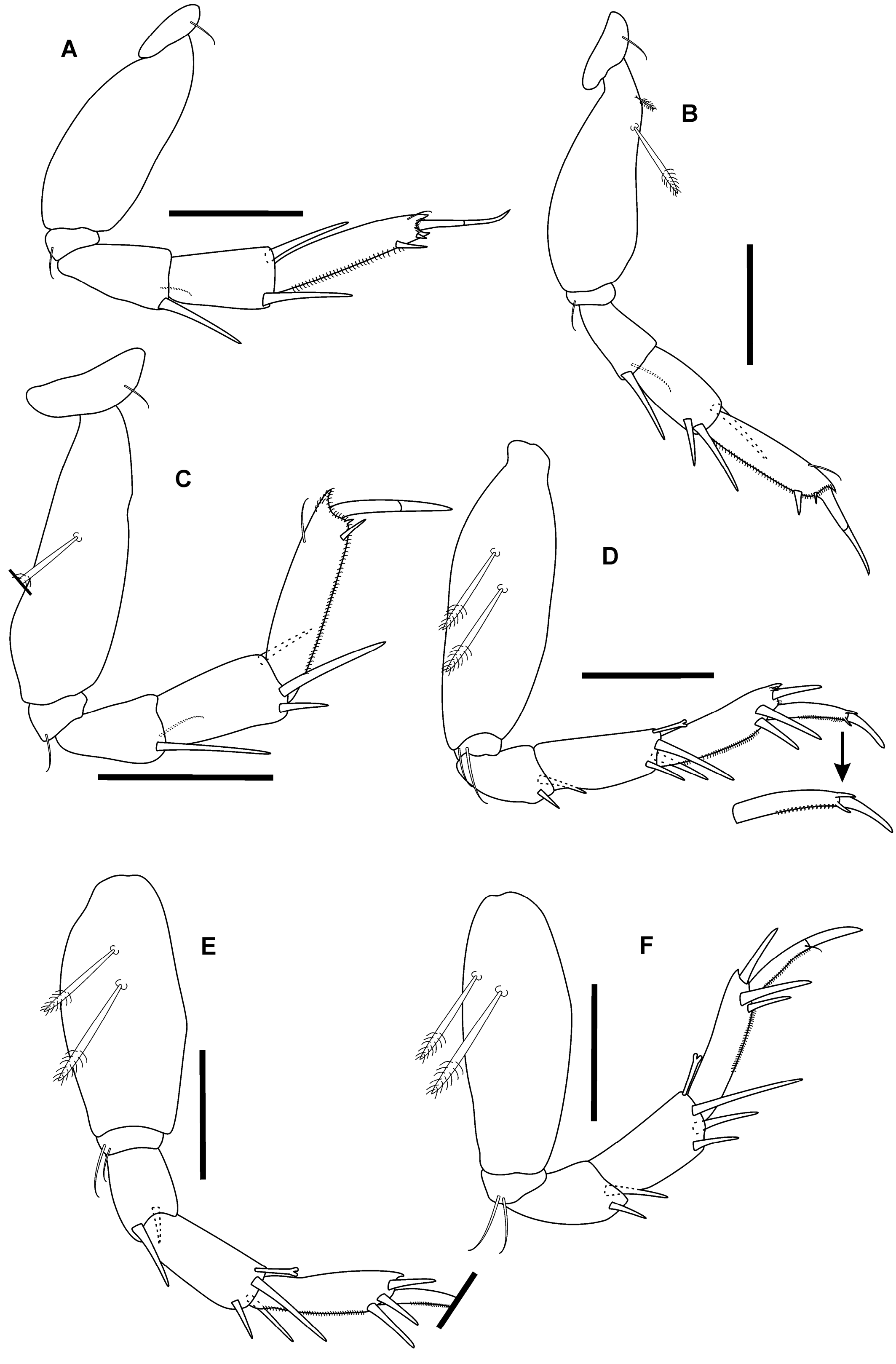


Figure 48. *Parakanthophoreus greenwichius* n. sp., female, paratype. (A), pereopod 1; (B), pereopod 2; (C), pereopod 3; (D), pereopod 4; (E), pereopod 5; (F), pereopod 6. Scale bar: 0.5 mm.

distal setae. Propodus more than half as long as basis, with ventral margin with numerous small spines, two ventrodistal spiniform setae and one spine both dorso- and ventro-distally, with small simple dorsodistal seta. Dactylus naked, about as long as unguis, combined half as long as propodus.

Pereopod 2 (Figure 48B) as pereopod 1 except: basis with one long and small setulose dorsoproximal setae. Carpus with three spiniform distal setae.

Pereopod 3 (Figure 48C) as pereopod 2.

Pereopod 4 (Figure 48D) coxa fused to body. Basis more slender than those of pereopods 1–3 (l/w ratio 2.6), with two dorsomedial setulated setae. Ischium with two setae. Merus shorter than carpus, widening distally, with two short, spiniform ventrodistal setae. Carpus only slightly shorter than propodus with three spiniform setae and one “bone-shaped” distal seta. Propodus with one spine and one spiniform seta dorsodistally, two ventrodistal spiniform setae and small ventral spines. Dactylus shorter than propodus, with two distal spines and two rows of small ventral spines; unguis clearly demarcated, less than half as long as dactylus.

Pereopod 5 (Figure 48E) as pereopod 4 (dactylus broken).

Pereopod 6 (Figure 48F) as pereopod 4 except: dactylus with distal simple seta.

Pleopods (Figure 46D) subequal. Endopod with one inner and twelve plumose outer setae. Exopod basal seta arising from incompletely fused rudimentary article and separated from other setae, with ten plumose outer setae of which the most distal is shorter and thicker than the adjacent ones.

Uropod (Figure 46E) longer than pleotelson. Basal article longer than exopod, naked. Endopod with two subequal [length] articles; article 1 with six simple distal and one setulated setae; article 2 with one simple seta, rest of setation broken. Exopod with two subequal [length] articles, half as long as first endopod article; article 1 naked; article 2 with one thick and one simple distal seta.

Remarks. This species can be separated from all other species of *Parakanthophoreus* by the heavy, medially serrated, ventral setae on the cheliped fixed finger. In addition, the short and thick antennules, the huge carpal shield, and the robust maxilliped setae, set this species apart from other recorded species of the genus except the Arctic species *P. inermis* (Hansen, 1913) which cannot possibly be present in the Antarctic.

Genus *Paraleptognathia* Kudinova-Pasternak, 1981

Amended diagnosis. Pleonite 5 without ventral spur. Pleotelson without lateral spines. Cheliped carpus, propodus, and fixed finger with extensive surface ornamentation; carpus with large carpal shield; fixed finger with proximal inner denticulations. Uropod basal article without accessory spur; uropod endopod article 1 without spur.

Type-species. *Paraleptognathia typicus* Kudinova-Pasternak, 1981.

Remarks. This genus also includes *P. bacescui* Kudinova-Pasternak, 1985.

Table 3. List of species in *Parakanthophoreus*, with mandatory spelling changes of species names to correspond with gender.

Previous species epithet	Authority	Species epithet after transfer to new genus
alba	Hansen, 1913	*albus*
antarctica	Vanhöffen, 1914	*antarcticus*
australis	Beddard, 1886	No change
benguela	Guerrero-Kommritz, 2004	No change
bisetulosa	Dojiri & Sieg, 1997	*bisetulosus*
brachiata	Hansen, 1913	*brachiatus*
crassicauda	Bird, 2007	*crassicaudus*
fastuosa	Guerrero-Kommritz, 2004	*fastuosus*
greenwichius	n. sp	No change
imputatus	Bird, 2007	No change
inermis	Hansen, 1913	No change
longiremis	Lilljeborg, 1864	No change
multiserratus	Hansen, 1913	No change
multiserratoides	Guerrero-Kommritz, 2004	No change
nanopsenos(*)	Bamber & Bird, 2009	No change
tenuichela	Guerrero-Kommritz, 2004	*tenuichelus*
verutus	Błażewicz-Paszkowycz, *et al.*, 2013	No change
vikingra	Błażewicz-Paszkowycz & Bamber, 2011	No change
weddellensis	Sieg, 1986	No change

(*)Probably represents a separate (and new) genus, but without the maxilla it is impossible to determine with certainty.

Acknowledgments

This paper is # 180 from the ANDEEP material. The authors are grateful to Professor A. Brandt, University of Hamburg for allowing the use of the material from the ANDEEP cruises. Thanks are also extended to Dr. Graham Bird for identifying most of the ANDEEP material to genus level and for a very constructive critique of the manuscript. The research of the senior author was partially supported by the European Regional Development Fund (ERDF) through the COMPETE—Operational Program Competitiveness and national funds through FCT—Foundation for Science and Technology, under the project PEst-C/MAR/LA0015/2011. This paper is part of a PhD dissertation (C.L.A.S.) funded by CAPES—Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Grant number: 5428/10-6).

References

Anderson, G. (2013). Tanaidacea Taxa and Literature. Available from: http://peracarida.usm.edu/ (accessed 15 February 2013)

Bamber, R.N., Bird, G.J., Błażewicz-Paszkowycz, M. & Galil, B. (2009). Tanaidaceans (Crustacea: Malacostraca: Peracarida) from soft-sediment habitats off Israel, Eastern Mediterranean. *Zootaxa*, 2109: 1–44.

Beddard, F.E. (1886). Report on the Isopoda collected by HMS Challenger during the years 1873–1876. Second part. *Challenger Report, Zoology*, 17 (1): 1–178.

Bird, G.J. (2007). Tanaidacea (Crustacea: Peracarida) from Japan III. The deep trenches; the Kurile-Kamchatka Trench and Japan Trench. Family *incertae cedis*. *Zootaxa*, 1599: 121–149.

Bird, G.J. (2011). Paratanaoidean tanaidaceans (Crustacea: Peracarida) from littoral and shallow sublittoral habitats in New Zealand, with descriptions of three new genera and seven new species. *Zootaxa*, 2891: 1–62.

Bird, G.J. & Holdich, D.M. (1984). New deep–sea leptognathiid tanaids (Crustacea, Tanaidacea) from the North-east Atlantic. *Zoologica Scripta*, 13 (4): 285–315. http://dx.doi.org/10.1111/j.1463-6409.1984.tb00044.x

Bird, G.J. & Larsen, K. (2009). Tanaidacean Phylogeny: The second step. The basal Paratanaoidean families. *Arthropod Systematics Phylogeny*, 67 (2): 137–158.

Błażewicz-Paszkowycz, M. & Bamber, R. (2009). A new genus of a new Austral family of paratanaoid Tanaidacea (Crustacea: Peracarida: Tanaidacea), with two new species. *Memoirs of Museum Victoria*, 66: 5–15.

Błażewicz-Paszkowycz, M. & Bamber, R. (2011). Tanaidomorph Tanaidacea (Crustacea: Peracarida) from Mud-Volcano and Seep Sites on the Norwegian Margin. *Zootaxa*, 3061: 1–35.

Błażewicz-Paszkowycz, M. & Bamber, R. (2012). The shallow-water Tanaidacea (Arthropoda: Malacostraca: Peracarida) of the Bass Strait, Victoria, Australia (other than the Tanaidae). *Memoirs of Museum Victoria*, 69: 1–235.

Błażewicz-Paszkowycz, M., Bamber, R. & Jóźwiak, P. (2013). Tanaidaceans (Crustacea: Peracarida) from the SoJaBio joint expedition in slope and deeper waters in the Sea of Japan. *Deep-Sea Research* II, 86–87: 181–213. http://dx.doi.org/10.1016/j.dsr2.2012.08.006

Bremer, K. (1994). Branch support and tree stability. *Cladistics*, 10: 295–304. http://dx.doi.org/10.1111/j.1096-0031.1994.tb00179.x

Dana, J.D. (1849). Conspectus Crustaceorum, Conspectus of the Crustacea of the U. S. Exploring Expedition. *American Journal of Science,* 2: 424–428.

Dojiri, M. & Sieg, J. (1997). The Crustacea Part 2. The Isopoda, Cumacea and Tanaidacea. The Tanaidacea. *In:* Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 11. Santa Barbara *Museum of Natural History,* Santa Barbara, pp. 181–278.

Goloboff, P., Farris, J. & Nixon, K. (2008). TNT, a free program for phylogenetic analysis. *Cladistic*, 24: 774–786. http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x

Gordon, D.P (2010). Species 2000. The New Zealand Inventory of Biodiversity; chapter 8, Subphylum, Crustacea. Vol. 2. Canterbury, University Press, Christchurch, pp. 164–166 & 223–224.

Guerrero-Kommritz, J. (2004). A revision of the genus *Paraleptognathia* Kudinova-Pasternak, 1981 (Crustacea: Tanaidacea) and description of four new species. *Zootaxa*, 481: 1–63.

Guerrero-Kommritz, J. (2005). Review of the genus *Chauliopleona* Dojiri and Sieg 1997 (Crustacea, Peracarida, Tanaidacea) and description of three new species. *Journal of Natural History*, 39 (16): 1177–1210. http://dx.doi.org/10.1080/0022293042000197586

Guerrero-Kommritz, J. & Brandt, A. (2005). Phylogenetic analysis of genera of 'Akanthophoreinae' (Crustacea: Tanaidacea). *Organisms Diversity & Evolution*, 5: 285–296. http://dx.doi.org/10.1016/j.ode.2004.12.005

Hansen, H.J. (1913). Crustacea, Malacostraca. II. IV. The Order Tanaidacea. *Danish Ingolf Expedition*, 3: 1–145.

Holdich, D.M. & Bird, G.J. (1985). A preliminary report on 'dikonophoran' tanaidaceans (Crustacea). *In:* Laubier, L. & Monniot, C. (ed.), Peuplements profonds du Golfe de Gascogne. Centre National de Tri d'Oceanographie Biologique, 441–447. [Ifremer, Brest].

Knight, J., Larsen, K. & Heard, R. (2003). Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico, XIII: A new deep-sea tanaidomorphan genus. *Proceedings of the Biological Society of Washington*, 116 (2): 497–502.

Krøyer, H. (1842). Nye Arter af Slægten Tanais. *Naturhistorisk Tidskrift*, 4: 167–188.

Kudinova-Pasternak, R.K. (1965). Deep-sea Tanaidacea from the Bougainville Trench of the Pacific. *Crustaceana*, 8: 75–91. http://dx.doi.org/10.1163/156854065x00578

Kudinova-Pasternak, R.K. (1970). Tanaidacea of the Kurile-Kamchatka Trench. Trudy Instituta Okeanologii, Akademiya Nauk SSSR, 86: 341–381.

Kudinova-Pasternak, R.K. (1976). Additional notes on the fauna of Tanaidacea (Crustacea, Malacostraca) of the deep water trenches. *Trudy Instituta Okeanologii,* Akademiya Nauk SSSR, 99: 115–125.

Kudinova-Pasternak, R.K. (1977). (*published in 1978). Tanaidacea (Crustacea, Malacostraca) from the deep-sea trenches of the western part of the Pacific. *Trudy Instituta Okeanologii*, Akademiya Nauk SSSR, 108: 115–135.

Kudinova-Pasternak, R.K. (1981). Benthos of the Submarine Mountain Markus Necker and Adjacent Pacific Regions. In: Kuznetsov, A.P. & Mironov, A.N. (Eds.), Tanaidacea. *Trudy Instituta Okeanologii*, Akademiya Nauk SSSR, Moscow, pp. 94–112.

Kudinova-Pasternak, R.K. (1984). Tanaidacea (Crustacea, Malacostraca) from the Sea of Japan. *Zoologicheskii Zhurnal*, 63: 828–837.

Kudinova-Pasternak, R.K. (1985). Tanaidacea (Crustacea, Malacostraca) collected on the summit and at foot of Great-Meteor Seamount. *Zoologicheskii Zhurnal*, 120: 52–64.

Lang, K. (1949). Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologie*, 42: 1–14.

Lang, K. (1971). Die Gattungen *Agathotanais* Hansen and *Paragathotanais* n. gen. (Tanaidacea). Crustaceana, 21: 57–71. http://dx.doi.org/10.1163/156854071x00229

Larsen, K. (2003). Proposed new standardized anatomical terminology for Tanaidacea (Peracarida). *Journal of Crustacean Biology*, 23: 644–661. http://dx.doi.org/10.1651/c-2363

Larsen, K. (2005). Deep-Sea Tanaidacea (Peracarida) from the Gulf of Mexico. *Crustaceana Monographs*, 5: 1–381.

Larsen, K. (2013). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited II: the family Anarthruridae and family incertae sedis, with descriptions of three new species and the erection of a new genus. *Zootaxa*, 3694 (4): 367–380. http://dx.doi.org/10.11646/zootaxa.3694.4.5

Larsen, K. & Shimomura, M. (2007). Tanaidacea (Crustacea: Peracarida) from Japan. II. Tanaidomorpha from the East China Sea, the West Pacific Ocean and the Nansei Islands. *Zootaxa*, 1464: 1–43.

Larsen, K. & Shimomura, M. (2009). Tanaidacea (Crustacea: Peracarida) from Japan. V. A new species of *Chauliopleona* from Nagasaki. *Species Diversity*, 14: 49–59.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny. The first step: The superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research,* 40 (4): 205–222. http://dx.doi.org/10.1046/j.1439-0469.2002.00193.x

Larsen, K., Bird, G. & Ota, M. (2013). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited I: the family Agathotanaidae Lang. *Zootaxa*, 3630 (3): 424–444. http://dx.doi.org/10.11646/zootaxa.3630.3.2

Lilljeborg, W. (1864). Bidrag till Kännedomen om de inom Sverige och Norrige förekommande Crustaceer af Isopodernas underordning och Tanaidernas familj.*Uppsala Universitet Årsskrifter*, 5: 1–32.

Sieg, J. (1976). Zum natürlichen System der Dikonophora Lang (Crustacea, Tanaidacea). *Zeitschrift für Zoologische Systematik und Evolutions forschung*, 14: 177–198.

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzeiger*, 205: 401–416.

Sieg, J. (1986). Tanaidacea (Crustacea) von der Antarktis und Subantarktis. II. Tanaidacea gesammelt von Dr. JW. Wägele wahrend der Deutschen Antarktis Expedition 1983*. Zoologischen Museum der Universität Kiel*, 2 (4): 1–80.

Sieg, J. & Dojiri, M. (1991). Two new species and a new genus of the suborder Tanaidomorpha (Crustacea: Tanaidacea) from Californian waters. *Journal of Natural History,* 25: 1495–1512. http://dx.doi.org/10.1080/00222939100770951

Vanhöffen, E. (1914). Die Isopoden der deutschen Südpolar Expedition 1901–1903. Deutsche Südpolar-Expedition. *Zoologie*. 15. Bd., Heft 7, 447–598. http://dx.doi.org/10.5962/bhl.title.10649

WoRMS (World Register of Marine Species). (2014). WoRMS taxon details. Available from: http://www.marinespecies.org/aphia.php?p=taxdetails&id=720033 (accessed 15 February 2014)

http://dx.doi.org/10.11646/zootaxa.3796.2.2

http://zoobank.org/urn:lsid:zoobank.org:pub:7B4A36F4-BFE3-4017-8F48-6499F95446C8

CHAPTER III. COMBINED MORPHOLOGICAL & MOLECULAR PHYLOGENIES

Article 7. Araújo-Silva, C.L., Larsen, K. & Froufe, E. (submitted). Tanaidacean (Crustacea: Peracarida) systematics revisited: A combination of morphological and molecular approaches. *Organisms Diversity & Evolution*.

Article 7. Tanaidacean (Crustacea: Peracarida) systematics revisited: A combination of morphological and molecular approaches

[1), 2)] Catarina L. Araújo-Silva, [3)] Kim Larsen & [1)] Elsa Froufe

[1)] Laboratory for Aquatic Ecology and Evolution, CIIMAR (Centro Interdisciplinar de Investigação Marinha e Ambiental), University of Porto, Rua dos Bragas, 289, 4050-123 Porto, Portugal. [2)] Capes Foundation, Ministry of Education of Brazil, Brasília–DF, 70040–020 Brazil. [3)] ENSPAC Department of Environmental, Social and Spatial Change, 11.2, Roskilde University Center. DK-4000 Roskilde, Denmark.

Abstract

Combined molecular and morphological phylogenetic analyses were constructed for the first time to evaluate the current systematics of Tanaidacea. These analyses were obtained from the combination of partial sequences of the molecular markers mtDNA COI, r28S, nuclear H3, as well as 112 morphological characters of 17 species belonging to eleven families of the two extant suborders. The phylogenetic analyses showed well supported clades for the Bayesian Inference, Maximum Likelihood, and Maximum Parsimony methods. Separate (morphology and molecular) and combined analyses showed that the superfamilies Paratanaoidea, Tanaoidea, Neotanaoidea, and Apseudoidea are well supported in individual clades. These results strongly suggest that the suborder Neotanaidomorpha should be restored and that both superfamilies Tanaoidea (Tanaidomorpha) and Paratanaoidea (Paratanaidomorpha new suborder) should each be elevated to suborder status. The analyses did not resolve most of the internal relationships for Paratanaoidea (Clade I) in both separate morphological and molecular phylogenies. Within Clade I, the family Colletteidae is found to be polyphyletic in all analyses, and the family Akanthophoreidae cluster with the genera *Chauliopleona*, *Biarticulata*, *Leptognathiella* and *Stenotanais* in both the molecular and combined analyses. The *incertae sedis* genus *Insociabilitanais* is transferred to Typhlotanaidae, while *Caudalonga* is transferred to *incertae sedis*. It was observed that the molecular data display a more robust phylogeny than the morphological dataset. It was also

observed that a more highly resolved and robust phylogeny emerges when a total evidence approach (i.e. combined morphological and molecular dataset) is employed.

Key words: Neotanaidomorpha, Paratanaidomorpha, Colletteidae, Peracarida, COI, 28S, H3.

Introduction

The order Tanaidacea is an order of crustaceans that belong to the superorder Peracarida. They are essentially marine and are commonly found from the intertidal zone to the deep-sea. In the deep-sea they can comprise up to 19% of the macrofauna and are here frequently the second most abundant Peracarida order found (Wolff 1977; Borowski 2001).

The systematics of Tanaidacea was firstly classified by Lang (1949) that divided it into two suborders: Monokophora and Dikonophora. Later, Sieg (1980), based on morphological characters renamed Monokophora as Apseudomorpha, while Dikonophora was separated into two suborders - Tanaidomorpha and Neotanaidomorpha. More recently, the systematics changed with the application of molecular analyses (Kakui *et al*. 2011) and since then, the order has been recognized as having only two extant suborders (i.e. Apseudomorpha and Tanaidomorpha) subdivided into four superfamilies (i.e. Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea) with altogether about 1,260 described species (Anderson 2013; WoRMS [accessed on December 2015]).

Tanaidacea is one of the most derived peracaridean taxa. This is mostly due to many morphological reversions and reductions, which have caused considerable systematics confusion. In an attempt to resolve these problems, many studies (mainly morphological phylogeny while less molecular) have been performed over the past fifteen years (e.g. Larsen & Wilson 2002; Bird & Larsen 2009; Drumm & Heard 2011; Bird 2012). Most of those studies agree that the tanaidacean systematics is complex and still poorly understood, mainly due to their high levels of homoplasy, excessive character reversals, high taxa numbers, and a general lack of stable characters for phylogenetic use. This is particularly true within the suborder Tanaidomorpha that, in fact, still lists about 35 genera as *incertae sedis* (Anderson 2013), highlighting the still unresolved phylogeny.

In order to mitigate those problems, many studies have attempted to revise the phylogeny of individual families. For instance, Larsen & Araújo-Silva (2014a) carried out a morphological phylogeny in order to resolve the systematics of Akanthophoreidae, known to display several problems (e.g. Sieg 1986; Guerrero-Kommritz & Brandt 2005). These authors established the family diagnosis and included genera that were previously listed as *incertae sedis* (i.e. *Mimicarhaphura*, *Stenotanais* and *Tumidochelia*). Another example is within suborder Apseudomorpha, where the monophyletic nature of families Apseudidae and Kalliapseudidae has also been disputed (Drumm & Heard 2011). These authors made a large revision on Kalliapseudidae, establishing several diagnoses and showing a monophyletic status of this family, but still with high levels of homoplasy.

The morphological approach is still without doubt the most common method used to infer Tanaidacea phylogenies. However, over the last decades the molecular techniques have been extensively used as an important complementary tool to resolve remaining uncertainties within the systematics of many crustaceans, consequently providing a valuable supplement in a broader perspective. Studies using molecular approaches on the Tanaidacea are still scarce, particularly are the deep-sea taxa often omitted. The first molecular phylogenetic analysis of Tanaidacea was published by Drumm (2010), based on the mitochondrial cytochrome *c* oxidase (COI) and two nuclear fragments, Histone 3 (H3) and 28S, but using only shallow-water taxa from the suborders Apseudomorpha and Tanaidomorpha. That analysis supported the old systematics but only the Tanaidomorpha presented strong support (Drumm 2010: 697, fig. 3). Later, Kakui *et al*. (2011) performed molecular analyses based on the rRNA 18S gene. These analyses showed close affinities between the Tanaidomorpha and Neotanaidomorpha and the latter was therefore reduced to superfamily rank and incorporated into Tanaidomorpha. This result conflicted with what has otherwise been deduced from morphological characters and the life history traits of these taxa. For instance, neotanaids are free-living surface dwellers (Gardiner 1975; Thistle *et al*. 1985), while tanaidomorphans are mostly, if not exclusively tube dwellers (Holdich & Jones 1983) thus, suggesting that studies of both taxa are needed. Although there are other molecular studies published, they are restricted to generic or species-specific issue (e.g. Drumm & Kreiser 2011; Kakui *et al*. 2012; Larsen *et al*. 2014).

As the phylogeny of Tanaidacea still remains poorly understood both on the morphological and molecular level, we aim in this study to resolve those problems by proposing: i) a new morphological phylogeny by adding new characters from recently described genera; ii) a new molecular phylogeny based on new sequences of the COI, 28S, and H3 partial fragments genes and including many deep-sea taxa; and iii) combining for the first time the morphological characters with the molecular data in order to increase the dataset of the Tanaidacea and most important analyze the relationships among the taxa.

Material and Methods

Taxa

Specimens were collected from deep Mid-Pacific Ocean (BIONOD/2012) and preserved in chilled 95% ethanol, stored at ≤ –20 ºC. From this collection, about 17 species (from 43 specimens) were identified morphologically prior to the molecular analyses (Table 4). A common problem found for those deep-sea samples was the often low number of individuals of each species (called *singletons*). Thus, to avoid problems with contaminations and loss of tissue we reduced to a minimum the manipulation/dissection of those specimens. Additionally, in many cases the whole animal had to be used for the DNA extraction, giving no possibility to score some characters (mainly from the mouthparts) in the morphological matrix (see below in Data section) and therefore most of the identifications are restricted to genus level.

Isopods were used as outgroups in the morphological, molecular and the final combined (morphological and molecular) datasets. Herein we include isopod species from three families: Asellidae, Idoteidae and Munnopsidae (Table 4). The Asellidae was chosen because it has a plesiomorphic position within Isopoda. On the other hand, Idoteidae and Munnopsidae are considered more derived and thus the three taxa present a representative span. We also decided to use these isopod taxa as they are from both deep and shallow waters in order to avoid problems from species with convergent evolution.

Morphology

Data

The data matrix consisted of 112 unordered and unweighted characters of 27 species that was first constructed in an Excel format (Appendices II and III) and then reformulated for use in PAUP4.0b10 (Swofford 1999). Some of those characters were verified and scored in the matrix by the authors' personal observations. However, some characters such as mouthparts among others, that for some reason needed to be dissected were scored based on the literature. In order to preserve some consistency in the analyses, some characters described herein correspond to those used in the phylogenies of Bird & Larsen (2009) and Larsen & Araújo-Silva (2014a). In addition, many new characters are added in order to include some of the recent described taxa.

Morphological phylogenetic analyses

Phylogenetic analyses were performed using two different methods: Bayesian Inference (BI) and Maximum Parsimony (MP). While MP has been commonly used in morphological tanaidacean phylogenies (e.g. Larsen & Wilson 2002; Bird & Larsen 2009) the Bayesian Inference method is much less used, although it can also be applicable to morphological data because the likelihood function forms the foundation of BI. Whereas likelihood methods seek to find the tree (and branch lengths) maximizing the probability of the observed data, Bayesian methods return the posterior probability, that is, the probability of the tree conditional on the observed data and the prior probability (the existing approaches specify equal prior probabilities for all possible trees) (Lewis 2001). Such an approach is likely to be more robust because it takes better account of the phylogenetic status quo (Huelsenbeck 2000).

Table 4. List of species analyzed with respective collection identification (Coll. ID), GenBank accession codes (COI, H3 and 28S) and information of suborder, superfamily and family affiliations. The Tanaidacea and outgroups taxonomic information follows Anderson (2013) and the website World Register of Marine Species (WoRMS - accessed on December 2015), respectively.

TAXA/GENE SEQUENCED	Coll. ID	COI	H3	28S
Order Tanaidacea Dana, 1849				
Suborder Apseudomorpha Sieg, 1980				
Superfamily Apseudoidea Leach, 1813				
Family Apseudidae Leach, 1813				
Leviapseudes sp.	T8	submitted	-	submitted
Family Kalliapseudidae Leach, 1813				
Mesokalliapseudes macsweenyi Drumm, 2003*		HM016211.1	HM016185.1	HM016189.1
Family Metapseudidae Lang, 1970				
Pseudoapseudomorpha sp.*		HM016208.1	HM016177.1	HM016194.1
Suborder Paratanaidomorpha Sieg, 1980				
Superfamily Paratanaoidea Lang, 1949				
Family Agathotanaidae Lang, 1971				
Paragathotanais sp.	T412	submitted	submitted	submitted
Family Akanthophoreidae Sieg, 1986				
Chauliopleona sp.	T396	submitted	submitted	submitted
Stenotanais sp.	T31	-	submitted	submitted
Family Colletteidae Larsen & Wilson, 2002				
Cheliasetosatanais spinimaxillipedus Larsen & Araújo-Silva, 2014	T409	submitted	-	submitted
Collettea sp.	T399	submitted	-	submitted
Caudalonga sp.	T407	-	submitted	submitted
Leptognathiella sp.	T405	-	submitted	submitted
Family Cryptocopidae (McLelland, 2008) Bird & Larsen, 2009				
Paraiungentitanais sp.	T400	submitted	submitted	submitted
Family Leptochelliidae Lang, 1973				
Leptochelia dubia (Krøyer, 1842)*		HM016215.1	HM016187.1	HM016199.1
Family Leptognathiidae Sieg, 1976				
Biarticulata sp.	T43	-	submitted	submitted
Leptognathiidae gen. sp.	T40	-	-	submitted
Family Nototanaidae Sieg, 1976				
Nototanais sp.*		-	HM016188.1	HM016196.1

TAXA/GENE SEQUENCED	Coll. ID	COI	H3	28S
Family Pseudotanaidae (Sieg, 1973) Sieg, 1976				
Pseudotanais sp.	T5	submitted	submitted	submitted
Family Tanaellidae Larsen & Wilson, 2002				
Arhaphuroides sp.	T411	submitted	-	submitted
Family Typhlotanaidae Sieg, 1984				
Typhlotanais sp.	T1843	submitted	submitted	submitted
Family incertae sedis Larsen & Wilson, 2002				
Armaturatanais sp.	T403	submitted	submitted	submitted
Parafilitanais sp.	T2367	submitted	submitted	submitted
Insociabilitanais sp.	T415	submitted	submitted	submitted
Suborder Neotanaidomorpha Sieg, 1980				
Family Neotanaidae Lang, 1956				
Venusticrus thor Araújo-Silva *et al*., 2015	T390	KT592232	-	KT592230**
Venusticrus thor Araújo-Silva *et al*., 2015	T391	KT592233	-	KT592231**
Suborder Tanaidomorpha Dana, 1849				
Family Tanaidae Dana, 1849				
Tanais dulongii (Audouin, 1826) *		KF928325.1	KF928332.1	KF928317.1
Zeuxo normani (Richardson, 1905) *		HM016203.1	HM016171.1	HM016197.1
OUTGROUP				
Order Isopoda Latreille, 1817				
Suborder Valvifera Sars, 1882				
Family Idoteidae Samouelle, 1819				
Idotea linearis (Linnaeus, 1766) *		JQ425515.1	-	JQ425586.1
Idotea sp. *		KC428828.1	KC428949.1	KC428847.1
Suborder Asellota Latreille, 1802				
Family Munnopsidae Lilljeborg, 1864				
Acanthocope galatheae Wolff, 1962 *		EF682285.1	-	EF682337.1
Family Asellidae Rafinesque, 1815				
Asellus aquaticus (Linnaeus, 1758) *		KR921859.1	AJ238321.1	KJ676729.1

* Taxa retrieved from GenBank

** Only primer 28SF works in the sequencing reaction

Thus, the BI analyses were performed using MrBayes version 3.2.3 (Ronquist *et al*. 2012). Analyses started with program-generated trees, with four heated Markov chains with default incremental heating. Two independent runs of four chains were started from a random tree for 5 X 10^6 generations, sampling every 1000 generations with a temperature setting of 0.5 producing a total of 100 000 trees, under the command (*DIMENSIONS NCHAR=112; FORMAT datatype=Standard)*.

The MP phylogeny was performed using PAUP4.0b10 (Swofford 1999). The characters were analyzed 'unweighted' and unordered. The analyses employ the tree space search of Edgecombe *et al*. (2000), with 1000 replications of random starting trees and heuristic TBR branch swapping on a maximum of 10 trees per replication, under the command (*hsearch start= stepwise addseq=random nchuck=100 chuckscore=2 nreps=1000 randomize=trees; hsearch start=current; nchuck=0 chuckscore=0*).

Molecular

DNA extraction to Sequencing

Genomic DNA was extracted from chelipeds and pereopods, except when individuals were too small (in those cases, the whole specimen was used). Total genomic DNA extraction, primers used, PCR reactions, and sequencing conditions are described in Larsen *et al*. (2014), except for: DNA template volumes of 1.0 µL or 1.5 µL for mtDNA COI and r28S; for nuclear H3 a volume of 0.5 µL was used. Due to the poor amplification success of the universal COI primers LCO1490 and HCO2198 (Folmer *et al*. 1994), a combination of primers CI-N-2191 (alias Nancy) (Simon *et al*. 1994) with LCO1490 (Table 5) was used. The cycle parameters were: initial denaturation at 94°C (3 min), denaturation at 94°C (30 s), annealing at 45°C (1 min for COI), 42ºC or 43 ºC (1 min for H3) and 45ºC–48ºC (1 min for 28S) and extension at 72°C (1 min 30s) repeated for 44 cycles, with a final extension time of 10 min at 72°C. Sequences were read on an ABI-310 (Table 5). A total of 18 sequences were successfully obtained and submitted to GenBank (Table 4).

Sequence Alignment

All chromatograms were checked manually using ChromasPro 1.7.6 (technelysium.com.au). The 28S sequences were aligned in MAFFT (Katoh & Toh 2008) using default parameters. Portions of hyper variable and other ambiguous regions in the 28S final alignment were eliminated from subsequent phylogenetic analyses using Gblocks (Castresana 2000). The coding genes sequences, COI and H3, were aligned using ClustalW (Thompson *et al*. 1994) implemented in Bioedit v.7.2.5 (Hall 1999). Furthermore, these sequences were translated in Bioedit into amino acids to search for stop codons that would be indicative of the presence of pseudogenes. Additionally, data from six tanaidacean species from shallow water and three isopods (outgroup) were retrieved from GenBank (see Table 4 for taxa and authorities) and included in the final alignments. In total 27 sequences were then adjusted manually. Polymorphic and Parsimony Informative sites, for each gene were obtained using DnaSP v5 (Librado & Rozas 2009).

Table 5. Gene names with their respective sequencing primer names and sequences; total length of the PCR product and in parenthesis the final alignment sequence analyzed for this study. Abbreviations: annealing temperature (AT); forward primer (F); reverse primer (R); base-pairs (bp).

Gene	Primer name and sequence	Product (analyzed)	AT
COI (Folmer *et al*. 1994)	LCO1490 (F) GTCAACAAATCATAAAGATATTGG HCO2198 (R) TAAACTTCAGGGTGACCAAAAAATCA	~ 631 bp	43–47 ºC
H3 (Colgan *et al*. 1998)	H3AF (F) ATGGCTCTGACCAAGCAGACVGC H3AR (R) ATATCCTTRGGCATRATRGTGAC	~ 308 bp	42–43 ºC
28S (Whiting 2002)	28S-RD1.3f (F) GGATTCCCTYAGTAAGKGCG 28S-rD4b (R) CCTTGGTCCGTGTTTCAAGAC	~ 493 bp	45–48 ºC
COI (alias Nancy) (Simon *et al*. 1994)	CI-N-2191 (R) CCCGGTAAAATTAAAATATAAACTTC	~ 631 bp	45–50 ºC

Models

The best-fit models of nucleotide substitution evolution were analyzed for the individual's genes (i.e. COI, 28S and H3). They were applied separately to each gene region and each codon position for the two coding genes (COI and H3) under the corrected Akaike Information Criterion (AIC), estimated by JModelTest 2.1.7 (Darriba *et al*. 2012).

For the COI dataset, for the first and the third position, the AIC selected model was the GTR+G (G = 0.6690; G = 0.4080, respectively), and for the second position GTR+I+G (G = 1.2410; I = 0.2340). For H3, models selected were, for the first position, GTR+G (G= 0.2980), for the second, SYM and for third, GTR+G (G = 1.7240). Finally, for 28S, the AIC selected model was the GTR+G (G = 0.5900).

Molecular phylogenetic analyses

Preliminary phylogenetic analyses were performed using three different methods i.e., Maximum Likelihood (ML), BI and MP, using the individual genes datasets. However, as all the retrieved phylogenies gave weak support values for most of the clades (data not shown), it was decided to analyze the combined molecular dataset, i.e. 28S+COI+H3. The ML tree was built using RAxMLGUI 1.3.1 (Silvestro & Michalak 2012). The proportion of invariable sites and the gamma distribution parameter were estimated by the program with a bootstrap analysis of 10 000 replicates. The BI were performed using MrBayes version 3.2.3 (Ronquist *et al*. 2012). Analyses followed the same default parameters described above in the morphological phylogenetic analyses. The MP method was performed in MEGA6 (Tamura *et al*. 2013) with the default settings: *bootstrap replications = 1000; gaps/missing data treatment = use all sites; MP search method = SPR; No. of initial trees = 10; MP search level = 1; Max. No. of trees to retain = 100*.

Combined Phylogenetic Analyses

The final molecular dataset (28S+COI+H3) included 27 sequences (1453 bp) and it was combined with the 112 morphological characters, totalizing 1565 of total evidence dataset. These analyses were performed with the defaults described above for the two phylogenetic analyses, BI and MP. Since the Maximum Likelihood method does not support morphological characters, it was not used here.

The BI analyses was carried out as described above, under the command (*DIMENSIONS NCHAR=1565; FORMAT datatype=mixed (Standard:1-112,DNA:113-1565)*. The MP analyses were performed in PAUP4.0b10 under the command (i.e. *hsearch start= stepwise addseq=random nchuck=100* *chuckscore=2 nreps=1000 randomize=trees; hsearch start=current; nchuck=0 chuckscore=0*;).

Results

Morphological Phylogeny

From the 112 characters analyzed, the BI and MP methods retained four separate and monophyletic clades, here named as Clades I–IV and respectively formed by superfamilies Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea (Figure 49A, B). In the BI, the nodes showed support values of posterior probabilities >70 (Figure 49A). While in the MP, the nodes showed lower support (data not shown) (Figure 49B).

The BI analyses showed Clade I supported (71), and divided *Leptochelia* from the deep-sea Paratanaoidea taxa. Inside this group, the relationships were predominantly politomies. The only supported group (84) was formed by *Caudalonga, Arhaphuroides* and *Paragathotanais*. The other Clades (II–IV) were better supported. The MP analyses generated four most parsimonious trees with equal length = 503; consistency index (CI) = 0.5547; homoplasy index (HI) = 0.6779; retention index (RI) = 0.5493. From the 112 characters, 95 were parsimony-informative. In these analyses, despite the relative high level of HI, all Clades were supported for at least one synapormorphy. Clade I (i.e. Paratanaoidea) was supported by one synapomorphy: the maxilliped basis fusioned. Two other characters contributed to the clustering of this Clade: three medial setae in second article of the maxilliped palp (CI = 0.818) and three or four medial setae in third article of the maxilliped palp (CI = 0.857). Clade II (i.e. Tanaoidea) was supported by two synapomorphies: pereopods 4–6 carpus with complex-denticulate setae and the marsupium structure with an ovisac. Clade III (i.e. Neotanaoidea) was well supported (99) and with one synapomorphy: the uropodal endopod article 1 with fine mid-length setae.

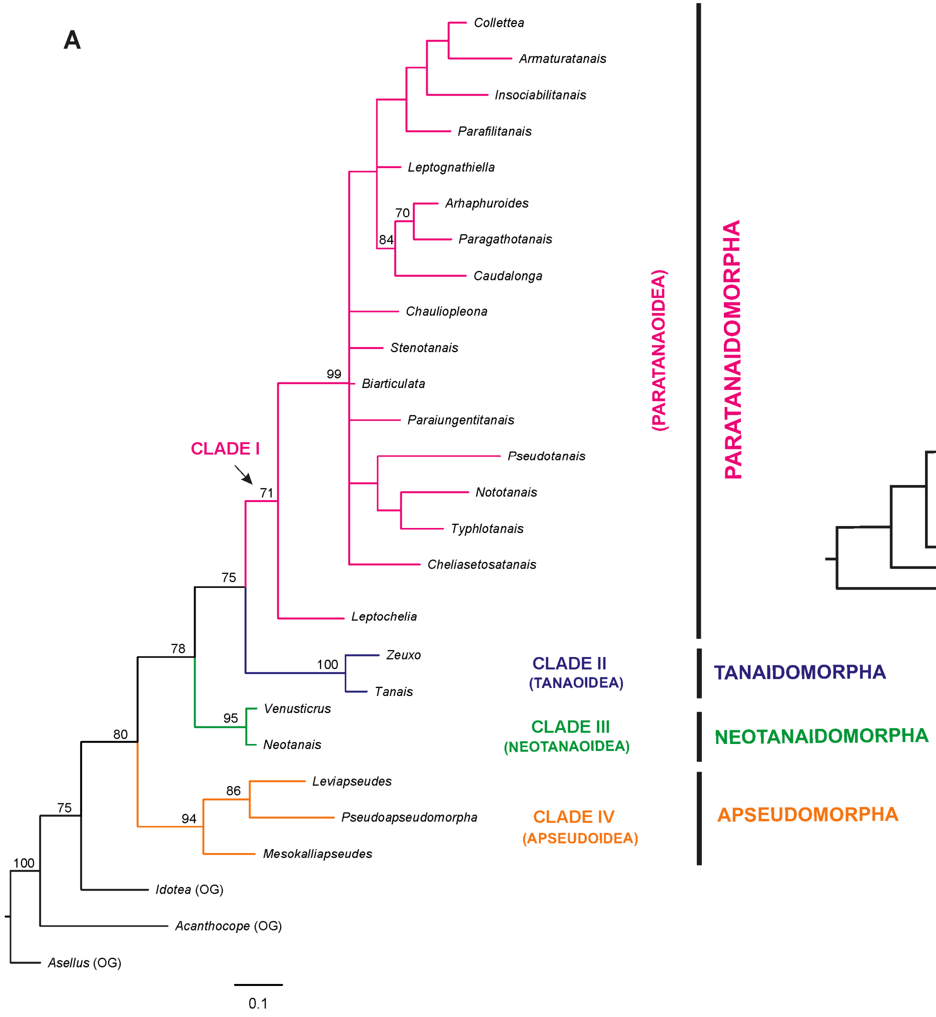
Finally, Clade IV (i.e. Apseudoidea) was supported by five synapomorphies: 1) the antennules biramous; 2) the antenna biramous; 3) rostrum shape; 4) the maxilliped endite with medial coupling hooks; and 5) pereopod 1 bearing a spiniform coxa.

Molecular Phylogeny

A total of 17 species from eleven families of Tanaidacea were successfully sequenced and analyzed for the three different genes. Results of the alignments with only new sequences (this study) or with the available sequences from GenBank (from each individual single gene as well as for the combined dataset) are illustrated in Table 6. Our dataset alignment (i.e. 28S+COI+H3), included 18 sequences, yielded 1453 bp in which 916 sites were variable and 706 sites parsimony informative. Together with the GenBank sequences, a total of 27 sequences were analyzed. This final alignment yielded 1453 bp in which 1115 sites were variable and 932 sites parsimony informative.

A single tree was recovered by ML and BI approaches that were congruent, revealing the same tree topology. BI phylogeny is shown in Figure 50. Most clades presented high supported values of posterior probabilities and bootstraps (>80 and 70, respectively). Similar to the morphological analyses, this phylogeny revealed the monophyletic status of all superfamilies, i.e, Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea (Clades I–IV, respectively; Figure 50). The first split in the phylogeny separated with high support (100/84) all Apseudomorpha taxa (i.e. Clade IV) from the other Tanaidacea (Clades I-III). These taxa are further divided, with high support (100/81), in two groups: one corresponding to Clade I (Paratanaoidea) and the other clustering Clade II (Tanaoidea) and III (Neotanaoidea) together. Thus, this molecular dataset shows that Clades II and III appeared closely related and well supported (100/87), but is further subdivided into two separated Clades, also well supported. Clade I was the most representative in our study. Interestingly, this group was well supported (100/100) and appeared divided into two groups. One small and well supported (100/100) only encompassing *Paraiungentitanais* and *Leptochelia*. This suggests that *Paraiungentitanais* could possibly be transferred to Leptocheliidae and that these two genera could possibly be raised to a superfamily. A second group, also well supported (100/77), formed by several deep-sea Paratanaoidea taxa, showed some politomies (Figure 50).

The MP analyses displayed the same phylogeny, but with lower bootstrap support values (data not shown).



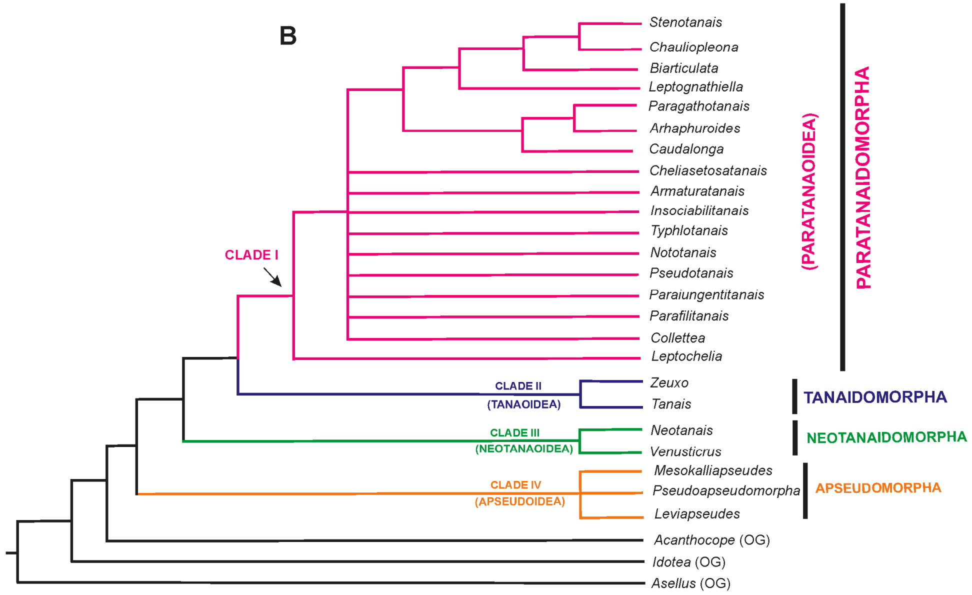


Figure 49. (A) Morphological phylogenetic tree obtained by the Bayesian Inference (BI) analyses from 112 characters; support values >70 are given as Bayesian posterior probability above nodes. **(B)** Maximum Parsimony (MP) strict consensus tree, resulted of four trees, from the character matrix data shown in Appendix III. Colored taxa names in upper case between parenthesis and labelling sidebars indicate, respectively, the superfamilies and suborders of Tanaidacea discussed in this work. For more taxa details see Table 4.

Table 6. Characteristics of the COI, 28S and H3 sequence alignments. Variable sites and parsimony informative of each individual gene (COI, 28S and H3) and the combined dataset (COI+28S+H3). On the left are the results for the 17 taxa sequenced for this study and on the right for the 27 taxa (see text for details). Abbreviations: bp = base pairs.

Gene	Alignment (bp)	Variable sites	Parsimony informative
COI	643 / 643	466 / 484	374 / 403
28S	502 / 502	327 / 403	227 / 327
H3	308 / 308	123 / 132	105 / 118
COI+28S+H3	1453 / 1453	916 / 1019	706 / 848

Combined Phylogenetic Analyses

Combined analyses of morphological (112) and molecular (1453) partitions resulted in a total of 1565 characters analyzed. Under equal weights, the MP analyses resulted in four most parsimonious trees with length = 5745; CI = 0.4181; HI = 0.6023; RI = 0.3964. From the 1565 characters analyzed, 943 were parsimony-informative. In both BI and MP analyses, the phylogeny recovered most clades (i.e. Clades I–IV, Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea, respectively) with high posterior probabilities and bootstraps values (>90/>70, respectively) (Figure 51A, B). Moreover, and although they were not congruent, both phylogenetic analyses supported and confirmed the monophyly of three groups formed by the superfamilies Paratanaoidea, Tanaoidea and Neotanaoidea (Clades I–III). The main difference was found in Clade IV. While in BI analyses the Apseudoidea was monophyletic and well supported (Figure 51A), in the MP both *Leviapseudes* and *Pseudoapseudomorpha* did not cluster with *Mesokalliapseudes* (Figure 51B). Similarly to the phylogenetic tree obtained only with the molecular data, all the Tanaidacea taxa were grouped in three main clades (Clades I–III) in both BI and MP (Figure 51A, B).

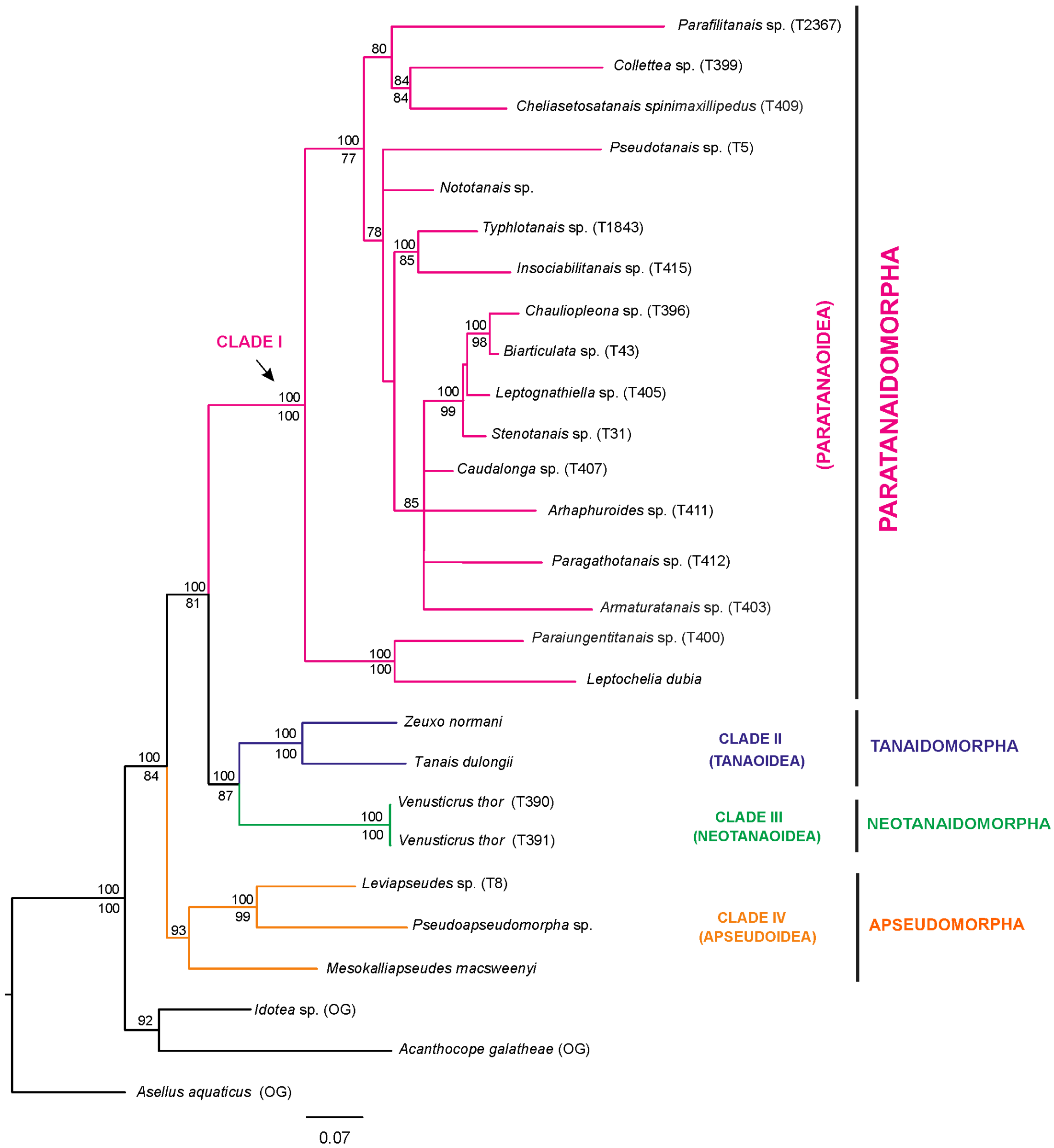


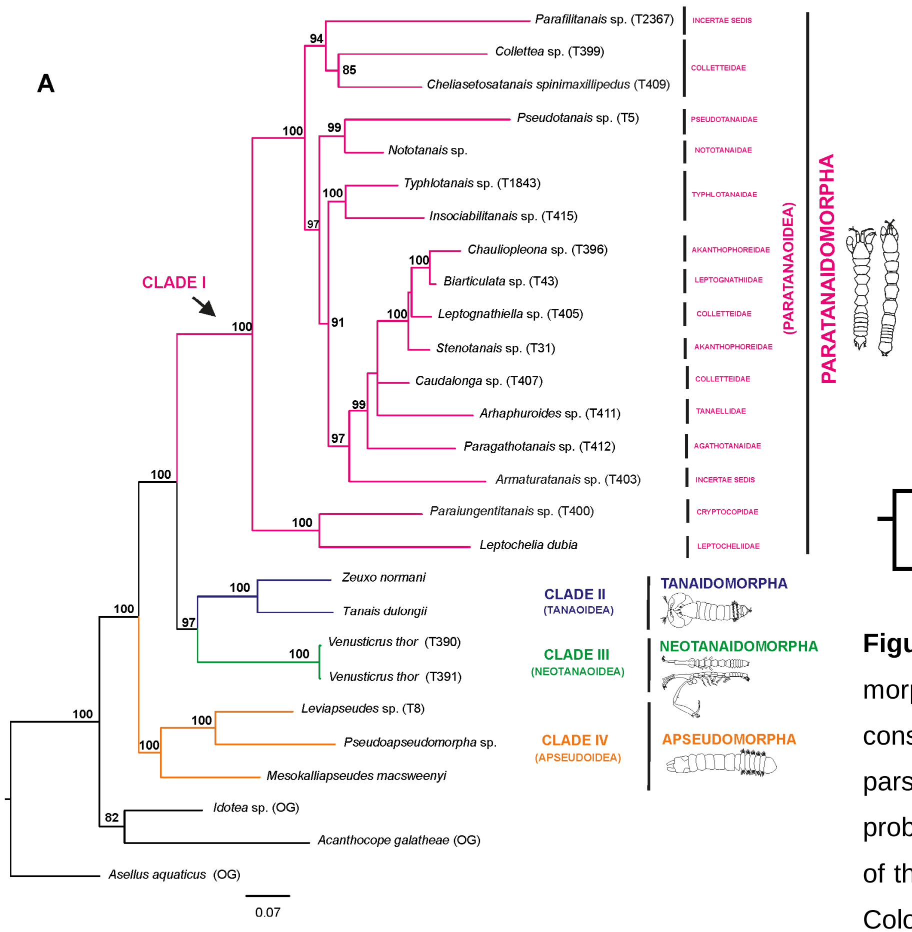
Figure 50. Phylogenetic tree obtained by the Bayesian Inference analyses (BI) of the molecular combined dataset (COI+H3+28S; 1453 bp) of Tanaidacea using Isopoda as outgroup. The tree topologies resulting from ML and BI approaches were congruent; only support values >70 are given, as Bayesian posterior probability above nodes and bootstrap support (ML) below nodes. Colored taxa names in upper case between parenthesis and labelling sidebars indicate, respectively, the superfamilies and suborders of Tanaidacea discussed in this work. For more taxa details see Table 4.

The BI phylogenetic analyses revealed that within Clade I the family Colletteidae is polyphyletic, as its four genera do not cluster together (i.e. *Collettea, Cheliasetosatanais, Leptognathiella* and *Caudalonga*). In fact, only *Collettea* and *Cheliasetosatanais* grouped forming the family Colletteidae, as it contains the type-genus (*Collettea*). The *incertae sedis* genus *Insociabilitanais* grouped with the type-genus *Typhlotanais* (99), thus suggesting the first to be included within Typhlotanaidae. A well supported clade (100) grouped by *Chauliopleona*, *Biarticulata, Leptognathiella* and *Stenotanais* suggests them to be all included in the Akanthophoreidae family. The genera *Pseudotanais, Nototanais, Arhaphuroides, Paragathotanais* and *Armaturatanais* appeared separated with no relationships. Clade I also supported a group formed by the *Paraiungentitanais* and *Leptochelia* (100) suggesting the first to be included within Leptocheliidae. Both Clades II and III appeared well supported (100) and as sister-clades (97).

As for the MP phylogenetic analyses, Clade I showed some unexpected results: i) a group formed by the two *incertae sedis* genera *Parafilitanais* and *Armaturatanais* (81); and ii) most of the other genera relationships are not resolved. The Clades II and III are well supported (both 100), but differently from the BI analyses they do not cluster together.

Discussion

In this study, the molecular phylogenetic tree (BI and ML; Figure 50) showed a better resolution than the morphological tree (BI and MP; Figure 49A, B). Despite that, the superfamilies Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea (Clades I–IV, respectively) were found to be monophyletic on both analyses. As expected, the combined analyses (i.e. molecular plus morphological data) showed a significant increase on the accuracy of the phylogeny and herein confirmed the monophyly of Clades I–IV (Figure 51A, B). These results, joint with the morphological characters and the life history traits of these taxa, e.g., neotanaids are free-living surface dwellers (Gardiner 1975) contrary to tanaidomorphans which are mostly, if not exclusively tube dwellers (Holdich & Jones 1983), led us to conclude that the suborder Neotanaidomorpha should be restored. The superfamilies Tanaoidea and Paratanaoidea, although both had been assigned inside the suborder Tanaidomorpha, both appeared well separated in this study.



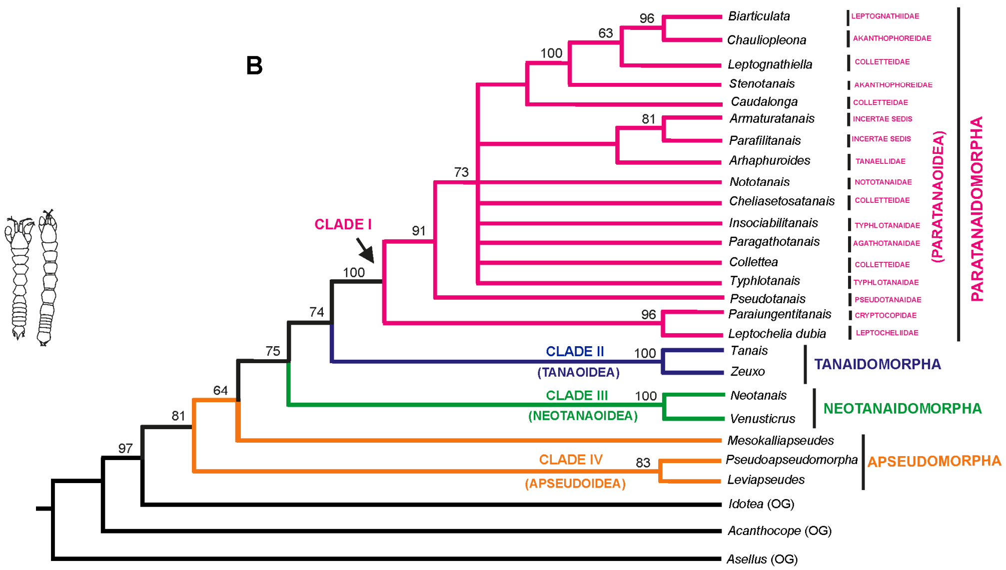


Figure 51. (A) Combined phylogenetic tree obtained by the BI analysis from 112 morphological characters and molecular dataset (COI+H3+28S; 1,453 bp) constructed by MrBayes; both summarize 1,565 characters, which 943 were parsimony-informative; support values >70 are given as Bayesian posterior probability above nodes. **(B)** Combined strict consensus tree of four trees resulting of the analysis of MP from the matrix in Appendix III; constructed by PAUP4.0b10. Colored taxa names in upper case between parenthesis and labelling sidebars indicate, respectively, the superfamilies and suborders of Tanaidacea discussed in this work. Pictured are the female and male of *Cheliasetosatanais spinimaxillupedus* modified from Larsen & Araújo-Silva (2014b: 3-4); followed by *Tanais dulongii* (Audouin, 1826), modified from Edgar (2008:7); male habitus of *Venusticrus thor* Araújo-Silva *et al*. (2015: 548) and female of *Mesokalliapseudes macsweenyi* modified from Drumm (2003:3).

As Tanaoidea showed to be more related to Neotanaoidea than to Paratanaoidea, we herein suggest to elevate them to suborder rank as Tanaidomorpha and Paratanaidomorpha (new suborder), respectively (Figure 52).

A diagnosis and identification key for the new classification is given herein.

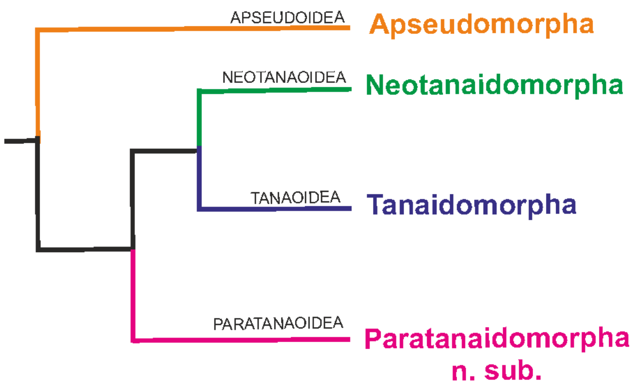


Figure 52. Phylogenetic hypothesis for Tanaidacea suborders proposed in this study, using combined analyses of morphological and molecular data. Paratanaidomorpha n. sub. = new suborder.

Morphological Phylogeny

Herein, Clades I–IV (BI and MP) were found to be monophyletic (Figure 49A, B), corroborating with the results obtained by the morphological phylogeny performed by Larsen & Wilson (2002). In our dataset, each Clade was supported by their own synapomorphy (described in the results). However, despite the addition of new characters and genera, in this dataset Clade I still showed most of its internal relationships unresolved. This is probably due to the high number of homoplastic characters (HI = 0.6779). This low resolution within Clade I was unexpected, since in previous phylogenies (e.g. Larsen & Wilson 2002; Bird & Larsen 2009) the relationships showed a better support. Herein, we believe that the use of several unrelated taxa or the addition of those with high levels of homoplastic characters (*incertae sedis* genera) could have had a profound influence in the final result, indicating that in the future more related genera should be used. Therefore, from these analyses we restrain to make any conclusions on the relationships of those taxa, as there are few or only one representatives of the each family. One well-supported relationship was found in the group formed by *Caudalonga*, *Arhaphuroides* and *Paragathotanais* that was not reported in previous published phylogenies (e.g. Larsen & Wilson 2002; Bird & Larsen 2009). Interesting, the MP analyses found this group sharing the characters of 'uropod exopod fused with basal article and bearing seta'.

Finally, the dichotomy seen among Tanaoidea and Neotanaoidea (i.e. Clades II and III) was not found. These differences might indicate that much more morphological characters and/or taxa must be included to show such similarity among Clades II and III.

Molecular Phylogeny

Overall, Clade I (Figure 50) showed some politomies, but also confirmed some supported groups of genera i.e., *Collettea* and *Cheliasetosatanais* (as family Colletteidae), *Typhlotanais* and *Insociabilitanais* (as family Typhlotanaidae). In addition, an interesting small clade formed by *Paraiungentitanais* and *Leptochelia* is seen, suggesting the first one to be included within the family Leptocheliidae. However, this arrangement is new and was not seen in previous morphological phylogenies (e.g. Larsen & Wilson 2002), therefore we restrain to make conclusions for now.

Clades II and III were found as sister-clades, corroborating the results performed by Kakui *et al*. (2011: 754, figs. 4-5). However, these authors joint them in one suborder (i.e. Tanaidomorpha) and in the present study we instead propose to raise each to an individual suborder. Our rationale for this division is based on the large genetic divergence shown between Clade I and Clades II and III (Figure 50). Because of these divergences and the well supported status of each of the Clades, we herein suggest re-erecting the former suborder Neotanaidomorpha (Neotanaoidea), elevating Paratanaoidea to suborder rank by the name Paratanaidomorpha, and keep a restricted Tanaidomorpha only encompassing the superfamily Tanaoidea.

Combined Phylogeny

In the present study, the combined molecular and morphological phylogenetic analyses resulted overall in rather similar results as those obtained by Kakui *et al*. (2011). One difference from Kakui *et al*. (2011) is that we included representatives of the four superfamilies, especially several Paratanaoidea taxa from the deep-sea, and this gave us more detailed information regarding the suborder arrangement. This should be considered for future tanaidacean phylogenies, since many Paratanaoidea taxa from the deep-sea are considered highly derived among tanaidaceans. After analyzing the morphological, molecular and the combining datasets, we concluded that all four superfamilies have diverged sufficiently and that each one is well supported and monophyletic; thus warranting their own suborder status. In addition, they are also supported by their own synapomorphies (described in results) (Figure 51A, B). The analyses of Kakui *et al*. (2011) only included molecular data, thus their classification did not consider the morphological characters shared by both Neotanaidomorpha and Apseudomorpha (e.g. maxillule with two developed endites; maxilla well developed, antennule with more than five articles). Interesting, according to Sieg (1980) classification, those sharing characters suggested that neotanaidomorphans could represent a linkage between the suborders Apseudomorpha and Tanaidomorpha. The closely relationship seen in the present study between Clades II and III was previously reported in morphological studies (e.g. Lang 1956; Gardiner 1975; Sieg 1986; Larsen & Wilson 2002). Thus, both molecular and the morphology phylogenies, together with the life history traits of these taxa, make us to believe that the superfamily Paratanaoidea should be removed from Tanaidomorpha (*sensu* Kakui *et al*. 2011) and that Neotanaoidea should not be incorporated in Tanaidomorpha as opposite to what was proposed by Kakui *et al*. (2011). Thus, herein we suggest that the former suborder Neotanaidomorpha should be restored and that both superfamilies Tanaoidea (Tanaidomorpha) and Paratanaoidea (Paratanaidomorpha new suborder) should each be assigned to suborder status.

The family Colletteidae was erected during a phylogenetic revision of the superfamily Paratanaoidea (Larsen & Wilson 2002). However, this family had weak support and was raised to assemblage genera from another family of Tanaidacea (i.e. Anarthruridae) (Larsen & Wilson 2002: 215). The present study, using BI, MP and ML phylogenetic methods revealed that Colletteidae is indeed polyphyletic, and the four genera used, did not cluster together (i.e. *Collettea, Cheliasetosatanais, Leptognathiella* and *Caudalonga*). The BI phylogenetic results of both the molecular and combined dataset (Figures 50 and 51A), confirmed type-genus *Collettea* clustering with *Cheliasetosatanais*, while in the BI and MP phylogenetic results based exclusively on morphological data, this relationship had no support (Figure 49A, B). Moreover, BI phylogenetic results of both the combined dataset and molecular data showed that the *incertae sedis* genus *Parafilitanais* clustering in a well supported clade with *Collettea* and *Cheliasetosatanais*, suggesting its inclusion in Colletteidae. However, this relationship must be further investigated, since the morphological character of 'lacking uropodal exopod' is not seen in any genera of Colletteidae and its systematics is still disputed.

Leptognathiella is remarkably well defined for a genus of the family Leptognathiidae (Larsen 2005). However, in the last revision of superfamily Paratanaoidea (i.e. Larsen & Wilson 2002), this genus clustered within family Colletteidae. In our phylogenetic analyses (BI of both molecular and combined dataset; Figures 50 and 51A), *Leptognathiella* clustered with a group of genera of the Akanthophoreidae-Leptognathiidae families (Figures 50 and 51A, B). With seven species described so far, *Leptognathiella* still needs more attention, and for now its position is left within Colletteidae, until more taxa are included. Finally, regarding *Caudalonga*, another Colletteidae genus, herein is not clustering together with type-genus *Collettea* and it is herein suggested to treat *Caudalonga* as *incertae sedis*.

The phylogenetic position of the family Akanthophoreidae was morphologically revisited and several genera (e.g. *Chauliopleona* and *Stenotanais)* were placed and confirmed in this family (Larsen & Araújo-Silva 2014a). In the present study, two Akanthophoreidae genera were sequenced, i.e. *Chauliopleona* and *Stenotanais*. In the molecular and combined phylogenies, the first clustered with *Biarticulata* (i.e. from family Leptognathiidae), confirming their previously reported morphological affinities (e.g. Guerrero-Kommritz 2005). Genus *Stenotanais* did not group with *Chauliopleona*, but appears in a well supported clade encompassed by the families Akanthophoreidae, Leptognathiidae and Colletteidae. Therefore, regarding this clade, both *Biarticulata* and *Leptognathiella* genera could possibly be transferred to the family Akanthophoreidae, maybe two different subfamilies could be erected. However, in order to clarify this, more taxa still needs to be compiled.

Regarding the genus *Insociabilitanais*, Larsen (2005) placed it as *incertae sedis*. This author described this genus as sharing morphological characters with taxa from several families (e.g. Typhlotanaidae, Agathotanaidae and Colletteidae). In the present study, *Insociabilitanais* was found grouping with *Typhlotanais*

(Figures 50 and 51A) with high support. In addition, despite this arrangement was not seen in the morphological phylogeny (Figure 49A, B), *Insociabilitanais* share characters with Typhlotanaidae by the following characters: uropods, general morphology of the mouthparts, and chelipeds among other characters. Therefore, both evidences suggest that *Insociabilitanais* should be transferred to the Typhlotanaidae.

The families Cryptocopidae and Leptocheliidae are represented in this study by the genera *Paraiungentitanais* and *Leptochelia*, respectively. The family Cryptocopidae was erected by McLelland (2008), later confirmed by Bird & Larsen (2009), and contains taxa mostly found in deep-sea environments. In contrast, Leptocheliidae is a family that occurs almost exclusively in shallow-water habitats (except for genera *Bathyleptochelia* and *Mesotanais*) (Edgar 2012). It is infamous for presenting morphological homogeneity among adult females and high degree of polymorphism within the species in the male stages (Larsen 2001). In the present study, except for the morphological phylogenetic analyses, these two genera, i.e. *Paraiungentitanais* and *Leptochelia*, clustered together and well supported (Figures 50 and 51A). This suggests that *Paraiungentitanais* should be included within the family Leptocheliidae. This evidence increases when previous studies (e.g. Larsen & Froufe 2013) have shown that within some species of *Leptochelia* the genetic distance is up to 29% (mtDNA COI unc. *p*- genetic distances), while the difference between *Paraiungentitanais* and *Leptochelia* found in the present study is only 34% (data not shown). However, as previously mentioned (see section molecular phylogeny above), this association is new and for now is left as it is until further taxa from both families should be evaluated.

Changes in the Systematics

The following diagnoses give the new classification for the suborders proposed in this study.

Diagnosis suborder Apseudomorpha. – (Modified after Larsen *et al*. 2015: 293). **Females.** Body cylindrical or dorsoventrally flattened, can be completely flattened with lateral spiniform extensions (e.g. Tanzanapseudidae). Antennule biramous or, very rarely, uniramous. Antenna biramous (or rarely uniramous), usually with

squama. Cheliped and pereopod 1 each often with small exopod. Pereopod 1 normally larger than the following pereopods. Uropods biramous, or very rarely uniramous. With four or five pairs of oostegites. **Male**. Recent males with a single large genital cone ventrally on pereonite 6. Simultaneous hermaphroditism reported for some genera (e.g. *Apseudes*). The mancae of some taxa (e.g. *Acutihumerus petronius* Araújo-Silva 2010, Kalliapseudidae, and Sphyrapodidae) have a small exopodite on pereopods 5 and 6 (Araújo-Silva & Larsen 2010).
Taxa included. All species of the superfamily Apseudoidea.

Diagnosis suborder Neotanaidomorpha. – (Modified after Larsen 2005: 96). **Female**. Eye-lobes present but never with visual elements. Always bearing pleopods. Antennule uniramous with 7–8 articles. Antenna without squama and with nine articles. Mandibles without palp, with strong and heavily calcified molars. Labium with two pairs of lobes and palp (more or less fused), both pairs of lobes and palp setose. Maxillule consisting of two endites with simple and specialized setae, palp missing. Maxilla well developed with multiple, specialized setae. Maxillipeds coxa and basis unfused; endites always separate and bearing several simple and specialized setae. Epignath strongly developed, divided into two almost equal-sized lobes and with setulose terminal seta. Chelipeds attached to cephalothorax by large sclerite, frequently larger than cheliped basis; small, incomplete ischium present. Pereopods all more or less similar and all of an unspecialized 'walking' type; coxae present on all pereopods; all pereopods without spinning glands. Pleopods biramous or uniramous (e.g. *Herpotanais*) and with plumose setae, endopod often biarticulate. Uropods biramous, endopod multi-articulate, with exopod with one or (normally) two articles. **Male**. Sexual polymorphism considerable. Antennae slimmer than in female but with same number of articles; antennule with numerous aesthetascs, in particular on article 4. Mouthparts reduced and non-functional. Cheliped carpus, dactylus, and fixed finger greatly enlarged in male. Uropods endopod article 1 with fine mid-length setae (reported in some species of *Neotanais* and *Venusticrus*).
Taxa included. All species of the superfamily Neotanaoidea.

Diagnosis suborder Tanaidomorpha. – (Modified after Larsen *et al*. 2015: 310 and Kakui *et al*. 2012: 138). **Female**. Body cylindrical. Eyes well defined with dark pigmentation except in *Protanais* and *Synaptotanais abyssorum*. Pleon of three to five free pleonites (if five, the last two reduced) and pleotelson. Antennule with 3–5 articles. Antenna with 6–8 articles. Mandibles with *lacinia mobilis* and setal row on both mandibles. Labium of two lobes and with or without terminal process (palp rudiment). Maxillule palp often biarticulate, with two to many setae. Maxilla rudimentary, oval in shape, often with individual setae. Maxilliped with coxa; coxae and bases not fused. Epignath strongly developed, kidney-shaped and setulose, with apical setulose seta. Cheliped ischium absent or present (in *Arctotanais*). Pereopod ischium absent or present (in *Arctotanais*); dactylus and unguis of pereopods 4–6 fused to a claw; with row of diagonal spines on both margins. Pleopods present with only three pairs, and only on the anterior pleonites, biramous, well developed or reduced. Uropods always uniramous and multiarticulate. Only one pair of ovisacs, arising from the coxae of pereopod 4. Hermaphroditism is not commonly found in this suborder, but was recently recorded in specimens of *Tanais dulongii* (Rumbold *et al*. 2015). **Male**. Mouthparts always retained. Sexual dimorphism restricted to cephalothorax, antennules, and chelipeds.

Taxa included. All species of the superfamily Tanaoidea.

Diagnosis suborder Paratanaidomorpha. – (Modified after Larsen *et al*. 2015: 301) **Female**. Eye-lobes present or absent. Antennule uniramous, with three to five articles. Antenna without squama and with zero (reduced) to seven articles. Mandibles without palp. Labium with one or two pairs of lobes. Maxillule consisting of one endite with simple, serrated, or bifurcate terminal setae, palp present and with one or two articles and always with two long terminal setae. Maxilla reduced, naked or with a few simple setae. Epignath slender, stick-like, with or without terminal seta. Maxilliped basis fusioned (except in family Leptocheliidae). Chelipeds attached to cephalothorax by a sclerite, pseudocoxa, or directly via basis; ischium absent. Pereopods 1–3 with spinning glands. Pereopod 1 often longer than other pereopods. Pereopods 2–3 more or less similar and of unspecialized ‘walking’ type; coxae usually present. Pereopods 4–6 usually of the clinging type, coxa most often missing. Pleopods biramous, uniramous (e.g. Pseudozeuxidae), or absent. Uropods uniramous (e.g. *Parafilitanais*) or biramous, endopod with zero articles (fused to basal article) to multi-articulate; exopod with two articles, one article, reduced to a spiniform process (e.g. *Paranarthrurella*), absent (e.g. families Agathotanaidae, Tanaellidae) **Male**. Sexual variation often in multiple characters. Mouthparts often non-functional. Pleopods always present.

Taxa included. All species of the superfamily Paratanaoidea.

KEY TO THE EXTANT SUBORDERS OF TANAIDACEA (MODIFIED AFTER LARSEN 2005)

1. Antennae biramous (or, very rarely, uniramous, usually with squama). Mandibular palp present. Maxillipedal endite with medial coupling hooks..**Apseudomorpha**

1a. Antennae uniramous. Mandibular palp absent. Maxillipedal endite coupling hooks absent..**2**

2. Antennule with seven articles. Antenna with nine articles. Maxillule with two endites. Maxilla well developed. Uropodal endopod with more than five articles (female)..**Neotanaidomorpha**

2a. Antennule with five or less articles. Antenna with eight or less articles. Maxillule with one endite. Maxilla reduced. Uropod endopod with five or less articles (female)...**3**

3. Antenna with seven or less articles (female). Right mandible without *lacinia mobilis.* Maxillule palp with two setae only. Maxilipedal basis fused (except Leptocheliidae). Epignath narrow and stick-like, often without terminal setae. Pereopod ischium always present. Female mostly with four pairs of oostegites (except Pseudotanaidae which have one). Uropod often biramous...**Paratanaidomorpha n. sub.**

3a. Antenna with eight or less articles. Right mandible with *lacinia mobilis.* Maxillule palp with more than two setae. Maxillipedal basis not fused. Epignath wide and always with terminal setae. Pereopod ischium missing (except in *Arctotanais*). Female with only one pair of ovisacs. Uropod uniramous, endopod always multiarticulate. ....**Tanaidomorpha**

Conclusions

Studies of molecular phylogeny in Tanaidacea are still very scarce, and increasing the number of this type of dataset, and particularly the combination of molecular and morphological data was the main goal. Thus, this is the first phylogeny of Tanaidacea that used a combination of molecular data (multi-gene approach) with morphology. It is also the first to include sequences from representatives of many deep-sea paratanaoidean taxa.

The molecular phylogeny gave a better resolution than the morphological tree but the combined analyses showed a significant increase on the accuracy of the phylogeny. The phylogenies of the morphological, molecular and the combined dataset showed that all four superfamilies (i.e. Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea) each is a well supported monophyletic group. In addition, they are also supported by their own synapomorphy, warranting suborder status. Therefore, we here remove Paratanaoidea from Tanaidomorpha and elevate it to suborder rank (i.e. Paratanaidomorpha). Also, the superfamily Neotanaoidea is restored to suborder rank (Neotanaidomorpha). Finally, Tanaoidea is elevated to suborder as well (i.e. Tanaidomorpha).

At the lower systematics level, our analyses support the following conclusions: 1) Colletteidae is polyphyletic and the genus *Caudalonga* is removed and considered *incertae sedis*. 2) Akanthophoreidae and Leptognathiidae are closely related and with the inclusion of further species might constitute one large family, including *Leptognathiella* and *Biarticulata*. 3) *Insociabilitanais* is included in the Typhlotanaidae, while *Parafilitanais* is maintained as *incertae sedis*.

Acknowledgements

This work is part of the senior author´s Ph.D. thesis (CLAS), funded by CAPES — Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (Grant number 5428/10-6). In addition, this research was partially supported by the European Regional Development Fund (ERDF) through the COMPETE - Operational Competitiveness Programme and national funds through FCT – Foundation for Science and Technology, under the project "PEst-C/MAR/LA0015/2014". The authors are grateful to Dr. George Wilson and another reviewer for the improvement of earlier versions of this manuscript. We also thank to Drs. Menot (IFREMER) and Rühlemann (BGR), chief scientists of the BIONOD expedition for inviting the junior author (KL) to participate in this cruise and for making the material available for study. The senior author also thank to Dr. Débora Lucatelli

(UFPE) for the help and Dr. Sahar Khodami from Senckenberg am Meer (German Center for Marine Biodiversity Research), for the kindness in helping with the use of primers.

References

Anderson, G. (2013). Tanaidacea-Thirty Years of Scholarship (Vers. 1.0, May, 2013), http://peracarida.usm.edu/TanaidaceaText.htm.

Araújo-Silva, C.L. & Larsen, K. (2010). Tanaidacea from Brazil. II. A revision of the subfamily Hemikalliapseudinae (Kalliapseudidae; Tanaidacea; Crustacea) using phylogenetic methods. *Zootaxa*, 2555: 30–48.

Araújo-Silva, C.L., Froufe, E. & Larsen, K. (2015). Two new species of family Neotanaidae (Peracarida: Tanaidacea) from the Antarctic and Mid-Pacific Oceans. *Zootaxa*, 4018 (4): 535–552.

Bird, G.J. (2012). A new leptochelioid family, Heterotanoididae (Crustacea: Peracarida: Tanaidacea), and a new species of *Heterotanoides* from New Zealand. *Zootaxa*, 3481: 1–26.

Bird, G. J. & Larsen, K. (2009). Tanaidacean Phylogeny–the Second Step: the Basal Paratanaoidean Families (Crustacea: Malacostraca). *Arthropod Systematics & Phylogeny*, 67(2): 137–158.

Borowski, C. (2001). Physical disturbed deep-sea macrofauna in the Peru Basin, southeast Pacific, revisited 7 years after the experiment impact. *Deep-Sea Research*, 48: 3809–3839.

Castresana, J. (2000). Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution,* 17: 540–552.

Colgan D.J., MacLauchlan A., Wilson G.D.F., Livingston S.P., Edgecombe G.D., Macaranas J., Cassis G., Gray M.R. (1998). Histone H3 and U2 snRNA DNA sequences and arthropod molecular evolution. *Australian Journal Zoology*, 46: 419–437. http://dx.doi.org/10.1071/ZO98048

Darriba, D., Taboada, G. L., Doallo, R. & Posada, D. (2012). jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods,* 9: 772.

Drumm, D. T. (2003). *Kalliapseudes* (*Mesokalliapseudes*) *macsweenyi*, a new species of Kalliapseudidae (Crustacea: Tanaidacea: Apseudomorpha) from mangroves in Florida*. Zootaxa,* 357: 1–12.

Drumm, D. T. (2010). Phylogenetic relationships of Tanaidacea (Eumalacostraca: Peracarida) inferred from three molecular loci. *Journal of Crustacean Biology*, 30: 692–698.

Drumm, D.T. & Heard, R.W. (2011). Systematic revision of the family Kalliapseudidae (Crustacea: Tanaidacea). *Zootaxa*, 3142: 1–172.

Drumm, D.T. & Kreiser, B. (2011). Population genetic structure and phylogeography of *Mesokalliapseudes macsweenyi* (Crustacea: Tanaidacea) in the northwestern Atlantic and Gulf of Mexico. *Journal of Experimental Marine Biology and Ecology*. doi:10.1016/j.jembe.2011.10.023.

Edgar, G. J. (2008). Shallow water Tanaidae (Crustacea: Tanaidacea) of Australia. *Zootaxa*, 1836: 1–92.

Edgar, G. J. (2012). New Leptocheliidae (Crustacea: Tanaidacea: Tanaidomorpha) from Australian seagrass and macro-algal habitats, and a redescription of the poorly-known *Leptochelia ignota* from Sydney Harbour. *Zootaxa*, 3276: 1–37.

Edgecombe, G.D., Wilson, G.D.F., Colgan D.J., Gray, M.R. & Cassis, G. (2000). Arthropod cladistics: combined analysis of histone H3 and U2 snRNA sequences and morphology. *Cladistics*, 16 (2): 155–203.

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. (1994). DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3: 294–299.

Gardiner, L. F. (1975). The systematics, postmarsupial development and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea). *Smithsonian Contribution to Zoology*, 170: 1–265.

Guerrero-Kommritz, J. & Brandt, A. (2005). Phylogenetic analysis of genera of ‘Akanthophoreinae’ (Crustacea: Tanaidacea). *Organisms, Diversity & Evolution,* 5: 285–296.

Hall, T. A. (1999). Bioedit: a user friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41: 95–98.

Holdich, D. M. & Jones, J. A. (1983). The distribution and ecology of British shallow-water tanaid crustaceans (Peracarida, Tanaidacea). *Journal of Natural History*, London 17: 157–183.

Huelsenbeck, J.P., Rannala, B. & Masly, J.P. (2000). Accommodating Phylogenetic Uncertainty in Evolutionary Studies. *Science*, 288: 2349–2350.

Kakui, K., Katoh, T., Hiruta, S.F., Kobayashi, N. & Kajihara, H. (2011). Molecular Systematics of Tanaidacea (Crustacea: Peracarida) Based on 18S Sequence Data, with an Amendment of Suborder/Superfamily - Level Classification. *Zoological Science*, 28: 749–757.

Kakui, K., Kobayashi, N. & Kajihara, H. (2012). Phylogenetic position of *Arctotanais* in the suborder Tanaidomorpha (Peracarida: Tanaidacea). *Journal of Crustacean Biology*, 32 (1): 127–139.

Katoh, K. & Toh, H. (2008). Recent developments in the MAFFT multiple sequence alignment program *Briefings in Bioinformatics, 9*, 286–298.

Lang, K. (1949). Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologie*, 42: 1–14.

Lang, K. (1956). Neotanaidae nov. fam. with some remarks on the phylogeny of Tanaidacea. *Arkiv för Zoologie*, 9: 469–475.

Larsen, K. (2001). Morphological and molecular investigation of polymorphism and cryptic species in tanaid crustaceans: implications for tanaid systematics and biodiversity estimates. *Zoological Journal of the Linnean Society*-London, 131: 353–379.

Larsen, K. (2005). *Deep-sea Tanaidacea (Peracarida) from the Gulf of Mexico* (pp. 387). Crustaceana Monographs 5. Leiden: Brill.

Larsen, K. & Araújo-Silva, C.L. (2014a). The ANDEEP Tanaidacea (Crustacea: Peracarida) revisited III: the family Akanthophoreidae. *Zootaxa*, 3796: 237–264.

Larsen, K. & Araújo-Silva, C.L. (2014b). A new genus of Colletteidae (Crustacea: Peracarida: Tanaidacea) from the Pacific with comments on dimorphic males with species specific characters. *Journal of the Marine Biological Association of the United Kingdom,* 94: 969–974.

Larsen, K. & Froufe, E. (2013). A new polymorphic species of *Leptochelia* (Crustacea: Tanaidacea) from Guinea Bissau, West Africa, with comments on genetic variation within *Leptochelia*. *African Invertebrates*, 54: 105–125.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny, the first step: the superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research,* 40: 205–222.

Larsen, K., Tuya, F. & Froufe, E. (2014). Genetic divergence of tanaidaceans (Crustacea:Peracarida) with low dispersal ability. *Scientia Marina*, 78: 81–90.

Larsen, K., Guţu, M. & Sieg, J. (†) (2015). Chapter 59. *Order Tanaidacea* Dana, 1849. Crustacea 5 (59): 249–328. Leiden.

Lewis, P.O. (2001). A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data. *Systematic Biology*, 50 (6): 913–925.

Librado, P. & Rozas, J. (2009). DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. *Bioinformatics,* 25: 1451–1452.

Mclelland, J.A. (2008). *A systematic and taxonomic review of the family Pseudotanaidae (Crustacea: Peracarida: Tanaidacea) based primarily on morphometric cladistic analyses*. Ph.D. Dissertation, Coastal Sciences, University of Southern Mississippi.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S. *et al*. (2012). MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice across a Large Model Space. *Systematic Biology*, 61: 539–542.

Rumbold, C.E., Obenat, S.M., Leonardi, M. S. & Spivak, E. D. (2015). Intersex in the gonochoristic crustacean *Tanais dulongii* (Audouin, 1826) (Peracarida: Tanaidacea: Tanaididae): a comparison of external reproductive characteristics, *Journal of Natural History*, 49 (13-14): 775–788. DOI: 10.1080/00222933.2014.981309

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzieger*, 205: 401–416.

Sieg, J. (1986). Distribution of the Tanaidacea: synopsis of the known data and suggestions on possible distribution patterns. *In:* Gore, R.H. & Heck, K.L. (eds.), Crustacean biogeography. *Crustacean Issues, 4* (pp. 165–194).

Silvestro, D. & Michalak, I. (2012). RaxmlGUI: a graphical front-end for RAxML. *Organisms Diversity & Evolution*, 12: 335–337.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994). Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the Entomological Society of America*, 87: 651–701.

Swofford, D.L. (1999). PAUP* – Phylogenetic Analysis Using Parsimony (and Other Methods), version 4.0 beta 10. – Sinauer Associates, Sunderland, Massachusetts.

Tamura, K., Stecher, G., Peterson D., Filipski A. & Kumar, S. (2013). MEGA6: Molecular Evolutionary Genetics Analysis, version 6.0. *Molecular Biology and Evolution*, 30: 2725–2729.

Thistle, D., Yingst, J.Y. & Fauchald, K. (1985). A deep-sea benthic community exposed to strong near–bottom currents on the Scotland Rise (western Atlantic). *Marine Geology*, 66: 91–112.

Thompson, J. D., Higgins, D.G., Gibson, T.J. (1994). CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gal penalties and weight matrix choice. *Nucleic Acids Research*, 22: 4673–4680.

Whiting M.F. (2002). Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. *Zoologica Scripta*, 31: 93–104. http://dx.doi.org/10.1046/j.0300-3256.2001.00095.x

Wolff, T., *et al.* (1977). Hadal life as analyzed from photographs. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 139: 263–336.

WoRMS (World Register of Marine Species). (2015). WoRMS taxon details. Available from: http://www.marinespecies.org/index.php (accessed 15 December 2015)

CHAPTER IV. GENERAL DISCUSSION

4. GENERAL DISCUSSION

In the present thesis, the knowledge of Tanaidacea was greatly improved by the analyses of several individuals from both shallow and deep waters collected from the Atlantic (Brazilian coast), Antarctic and Pacific Oceans. The results obtained increased the morphological data of Tanaidacea by adding several new descriptions, illustrations, and new morphological characters. Additionally, this thesis also greatly improved the molecular data available for this group, by including several new sequences from deep-sea representatives as well as from genera that were considered as *incertae sedis*.

Several questions related to the taxonomic, systematics, morphological and molecular phylogenies were addressed. In order to answer these issues, the results obtained in this thesis are divided in two main Chapters: II and III. Chapter II had as the main goal to morphologically analyze several taxa of Tanaidacea **(Articles 1–6)**. In Chapter III, the central goal was to test the current suborder classification and to propose a new comprehensive phylogeny for Tanaidacea based on both morphological and molecular data **(Article 7)**.

A total of 349 individuals were here identified. These specimens were subsequently placed in 16 families, 43 genera and 61 species of Tanaidacea. From the 61 identified species, eleven are new: *Apseudes noronhensis, A. aisoe, Neotanais bicornutus, Venusticrus thor, Paratanais coelhoi*, *Makraleptochelia potiguara, Intermedichelia jesseri, Cheliasetosatanais spinimaxillipedus, Chauliopleona ciimari, C. andeepi* and *Parakanthophoreus greenwichius*. Three new genera: *Makraleptochelia, Cheliasetosatanais* and *Parakanthophoreus* were also erected and described. All detailed information regarding these new taxa, i.e. descriptions, illustrations, discussion and their geographic records (if new), are presented in Chapter II **(Articles 1–6).**

A total of 80 specimens of Tanaidacea were analyzed from the Atlantic (Brazilian coast, REVIZEE-NE program). From these, seven families, nine genera and ten species were identified, which resulted in the erection of one new genus: *Makraleptochelia;* and five new species: *Apseudes aisoe, A. noronhensis, Makraleptochelia potiguara, Intermedichelia jesseri* and *Paratanais coelhoi* (Chapter II, **Articles 1–3**). In addition, four genera i.e., *Apseudes*, *Biarticulata*, *Nototanoides* and *Arhaphuroides* were recorded from the Brazilian coast for the first time. The Paratanaidomorpha was the most representative suborder, while the Neotanaidomorpha was not represented at all (for details see Appendix IV).

Regarding the Antarctic Ocean (ANDEEP I-III program) a total of 152 specimens were analyzed. From these, eleven families, 24 genera and 36 species were identified and resulted in the description of four new species: *Neotanais bicornutus*, *Chauliopleona ciimari, C. andeepi* and *Parakanthophoreus greenwichius;* and one new genus: *Parakanthophoreus* (**Articles 5 and 6**). Additionally, six taxa, i.e., *Tanaella kroyeri, Tanaella* cf. *prolixcauda, Armaturatanais, Parafilitanais, Portaratrum* and *Insociabilitanais*, were recorded from the Antarctic Ocean (see details in Appendix V) for the first time. Again, the Paratanaidomorpha was the most representative suborder (Appendix V).

Finally, from the Mid-Pacific Ocean (BIONOD/2012 campaign) a total of 117 specimens were analyzed. From these, ten families, 35 genera and 41 species of Tanaidacea were identified, from which two species, *Venusticrus thor* and *Cheliasetosatanais spinimaxillipedus*, and one new genus, *Cheliasetosatanais*, were fully described and illustrated (**Articles 4 and 5**). Additionally, eight taxa, i.e., *Glabroapseudes, Venusticrus, Paraiungentitanais, Armaturatanais, Caudalonga, Leptognathiella, Insociabilitanais* and *Pulcherella*, were recorded from the Pacific Ocean for the first time and four other genera, *Leviapseudes, Parafilitanais, Portaratrum* and *Paratyphlotanais*, for the North Pacific (see details in Appendix VI). As for the REVIZEE-NE and ANDEEP I-III programs, the Paratanaidomorpha was again the most representative suborder (Appendix VI).

A phylogenetic revision of the family Akanthophoreidae, based on the morphological data (including new characters), was done in Chapter II (**Article 6**), that led to several changes in the systematics of this family.

The current classification of Tanaidacea was revisited in Chapter III (**Article 7**). This was addressed through phylogenetic analyses obtained from both morphological and molecular data combined. For the morphological data, ten new characters were added, while for the molecular, 45 new sequences from 17 species were obtained for three genes: cytochrome *c* oxidase 1 (COI), nuclear large subunit ribosomal DNA (28S rRNA) and nuclear Histone 3 (H3). Phylogenetic analyses from the combination of these datasets were generated, resulting in a new classification for the Tanaidacea suborders: Neotanaidomorpha is re-erected and Tanaidomorpha (*sensu* Kakui *et al*. 2011) is splitted into Tanaidomorpha and a newly suborder Paratanaidomorpha (Chapter III, **Article 7,** Figure 52). The results of this thesis are thus contesting the current systematics of Tanaidacea proposed by Kakui *et al*. (2011). Furthermore, the results from these phylogenetic relationships also suggested some changes in the systematics of the families Typhlotanaidae and Colletteidae.

4.1. Tanaidacean new distribution records and biodiversity

The Tanaidacea encompasses about 1,260 described species (Anderson 2013), from which more than one-third were described in the past fifteen years alone (Figure 53). This may be related to the increase of the surveys in the deep-sea area as well as in other traditionally less explored regions (e.g. Brazilian coast). Nevertheless, the true tanaidacean biodiversity is probably still underestimated. The results obtained here well illustrate this assumption since among the 349 individuals analyzed, eleven were new species, three new genera and 22 taxa had their geographic distribution expanded for the first time in their respective study areas (for details, see Appendices IV–VI).

An example is the Brazilian coast (Atlantic) where studies about Tanaidacea have increased during the last years but still do not give a clear picture of its true biodiversity. In this thesis, four new records and five new species (Appendix IV) were recorded from this area, thus raising the number of recorded species from 43 to 52. Additionally, several unsorted tanaid samples, many from the deep-sea, are deposited in national and local Brazilian museum collections. A preliminary observation of these samples suggests that the current number of species could increase up to 150 (personal observation).

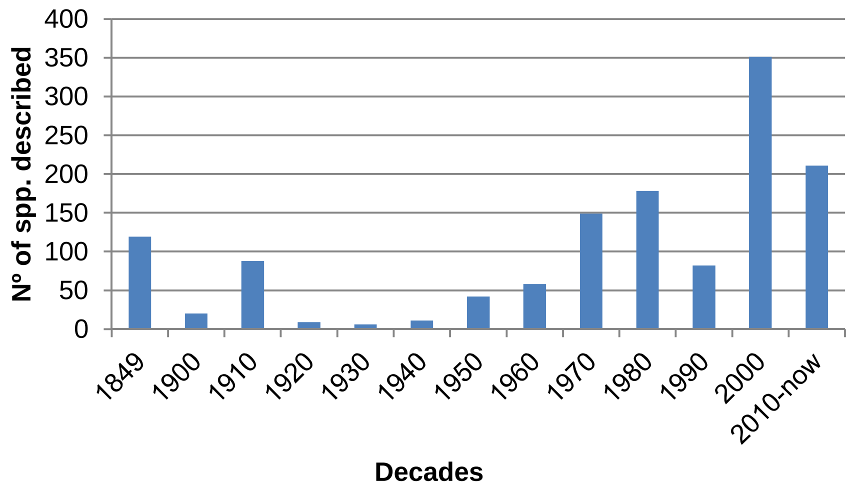


Figure 53. Number of new species described since the establishment of the order Tanaidacea.

A total of 18 genera identified from the Antarctic, were also found in the Mid-Pacific Ocean (Appendices V and VI). In fact, most deep-water genera seem to have representatives in all major oceans (Larsen 2005). This may be explained by evolution in a time where the Antarctic and Pacific Oceans could exchange taxa. Another explanation is that during the Oligocene and Miocene, climatic deterioration could have caused the extinction of many benthic taxa in the Antarctic (Feldmann & Tshudy 1989). Due to this event many ecological niches became available for well- or pre-adapted organisms, such as peracarids, which thrive in Antarctic (Brandt 1992). However, since Mid-Tertiary times the exchange of Antarctic species with species of neighboring continents has been severely restricted by distance and strong currents south of the Antarctic Convergence (Brandt 1992).

Finally, four genera collected from the Mid-Pacific Ocean are also found in the Gulf of Mexico (Appendix VI). Some have explained this by migration through the Isthmus of Panama and along the Yucatan Peninsula (Sieg 1986). Bamber & Sheader (2003) also suggested the migration of the Tanaidacea genus *Pakistanapseudes* in southern China and its occurrence in the deep-sea of Gulf of Mexico and Brazil through the Isthmus of Panama.

4.2. Taxonomy of Tanaidacea and problems caused by reproduction strategies

Taxonomy is the science of species identification and classification. It is considered the fundament for the study of any specific- or group of organisms in any field of Biology.

In tanaidaceans, reproductive strategies involve either separate sexes or hermaphroditism. The question of hermaphroditism is further divided in to two types: simultaneous- when the individuals are found with both a penal cone and oostegites, or sequential- when the individuals changes sexes from female to male, termed protogynic hermaphroditism (Kakui & Hiruta 2013; Rumbold *et al*. 2015). Protogyny involves strong female/male polymorphisms often combined with high morphological similarities between females of different species. The difficulty with the taxonomic identifications has been often linked to the amount of morphological variation related to this reproductive strategy. Among the eleven new described species in this thesis, five had both genders described. This allowed us to observe the morphological variations and make some remarks regarding their sexual dimorphisms.

The males and females of Leptocheliidae and Neotanaidae (i.e. *Makraleptochelia potiguara* (Figures 12A and 15A), *Neotanais bicornutus* (Figure 34A, F) and *Venusticrus thor* (Figures 36A and 38A), displayed strong sexual dimorphism in their general body shape. The males of these species are all characterized as having reduced or absent mouthparts, which is commonly reported for these families and others where the male is heavily dimorphic (e.g. Nototanaidae, Typhlotanaidae, Paratanaidae). Regarding the new Colletteidae species here described (i.e., *Cheliasetosatanais spinimaxillipedus*), the sexual dimorphism was expressed in a typical 'swimming-male', but with a fully developed labrum and maxilliped, almost identical to that of the female (see Figures 29E, 30 E and 31E, F). This is rare in paratanaidomorphans and is a novelty in Colletteidae, since the males of this family are known to retain functional mouthparts (Larsen & Wilson 2002). Developed labrum and maxilliped in mature, otherwise non-feeding males, have only been reported for the family Anarthruridae (i.e. genus *Siphonolabrum* Lang, 1971) and to a much less degree in the male of the leptocheliid *Makraleptochelia* (Figure 16C).

As the genders of taxa with heavily dimorphic males like 'swimming males do not share evident species-specific characters, it is extremely difficult to establish con-specificity of the genders of a given species (Bird & Larsen 2009). When such identifications of con-specific males and females have been assigned, it has often been on the basis of just finding them in the same sample (Suárez-Morales *et al.* 2004). It is entirely possible that some species-specific characters have been overlooked, but only by application of genetic methods can such identifications be verified (e.g. Błażewicz−Paszkowycz *et al*. 2014). Thus, in the future it is strongly recommend using these methods when dealing with such problematic taxa.

Among the superorder Peracarida, the Simultaneous Hermaphroditism (SH) is reported only for Tanaidacea (Kakui & Hiruta 2013). However, studies concerning SH for this group are still rare. In Tanaidacea records are commonly reported through a morphological observation (e.g. Lang 1953; Larsen *et al*. 2011) and rarely through histological study (e.g. Kakui & Hiruta 2013). This type of reproduction is found in several members of the suborder Apseudomorpha, although most of them are gonochoristic (Sieg 1984). In the present thesis, a large number of specimens belonging to the genus *Apseudes* were studied (Figures 22 and 26). Through a morphological examination of these individuals, it was possible to observe the SH condition for *Apseudes*, corroborating what was suggested by Larsen *et al.* (2011). A histological study in specimens of *Apseudes* also confirms the presence of the SH condition in the genus (Kakui & Hiruta 2013). These authors reported that the ovaries and testes could be simultaneously functional and even capable of self-fertilization, although the presence of oostegites, large chelae, and genital cones could also indicate only occasional SH. Thus, histological studies are necessary to determine the maturation and functionality of testes and ovaries (Rumbold *et al*. 2012).

These issues, together with their small sizes, confused systematics, and ontogenetic variations explain why tanaidaceans are considered one of the most difficult crustacean groups to identify at species and higher levels. This is probably the reason why they are often neglected in many ecological and biodiversity studies.

4.3. Systematics changes based on morphology

Herein is presented a brief discussion with additional morphological information and changes for each family systematics studied in detail in Chapter II **(Articles 1–6).**

Family Paratanaidae (Article 1)

According to the WoRMS website (accessed November 2015), the family Paratanaidae comprises twelve genera and 28 species, already including *Paratanais coelhoi* described in this thesis. The only previously recorded species from the Brazilian coast is *P. oculatus* (Vanhöffen, 1914 *sensu* Silva-Brum 1973).

In the present thesis a list of the main diagnostic characters (Bird 2011) is provided in Table 1 comparing *P. coelhoi* with the other species of *Paratanais*. Morphological comparisons of *P. oculatus* (*sensu* Silva-Brum 1973) and *P. coelhoi*, revealed some doubts concerning their separation. This was due to a high number of shared characters. Adding to the concern is the wide distribution of *P. oculatus* that was otherwise recorded from the Falkland and Kerguelen Islands (type-locality), Subantarctic and Indian Ocean. This led us to conclude that such global distribution of a shallow-water species, with limited swimming capacity is unlikely. Thus, it is possible that the identification of *P. oculatus* made by Silva-Brum (1973) is a mistake (Sieg 1986). However, this material is deposited in the 'Museu Nacional do Rio de Janeiro (MNRJ)', and could not be obtained for close examination. Therefore, without a full examination of the specimens described by Silva-Brum (1973) we herein maintain *P. coelhoi* and *P. oculatus* (*sensu* Silva-Brum 1973) as a separate species.

Family Leptocheliidae (Article 2)

In the last phylogenetic analyses, Bird & Larsen (2009) found at least five *incertae sedis* genera within Leptocheliidae; one of them was *Intermedichelia*. Bird & Larsen (2009) considered the character 'pereopods 4–5 propodus with modified dorsodistal setae' [character 94], which is found in *I. gracilis* as diagnostic for the genus (Gutu 1996: 117; fig. 40A, B). However, in the new species *I. jesseri*, described in this thesis, this character showed significant variation, and is therefore considered homoplastic (Chapter II, **Article 2,** Figures 19D and 20A). This change is further confirmed in this Chapter (heading 4.4)

Cryptic species are commonly found in Leptocheliidae genera, but most often reported in *Leptochelia* (e.g. Larsen & Froufe 2013). Similar to *Leptochelia* several individuals of both *I. gracilis* and *I. jesseri* were collected from the same stations. Thus, although the two *Intermedichelia* species show morphological differences, they also share many characters, mainly in general body morphology, to the point of suggesting them as cryptic species.

Family Apseudidae (Article 3)

The family Apseudidae is the largest tanaidacean family with about 200 described species (Anderson 2013), corresponding to almost one-third of all the taxa of all species in the suborder Apseudomorpha (Gutu 2006). In the present thesis, two new species are described: *Apseudes noronhensis* and *A. aisoe*. A close morphological examination of several specimens of *A. aisoe* made it possible to propose some changes in the systematics of Apseudidae **(Article 3).**

Gutu (2006) separated the genera *Muramurina* and *Androgynella* from *Apseudes* based mainly on the character of SH. However, this character is also found in the type-genus *Apseudes* (Larsen *et al.* 2011). In order to check the validity of *Muramurina* and *Androgynella* the diagnostic characters described by Gutu (2006) were compiled and, together with several new additional ones, are described in this thesis (see details in Chapter II, **Article 3**; Table 2, p. 101). The analyses of these diagnostic characters allowed us to conclude that *A. aisoe* is closely related to the former genus *Muramurina*, as well as to the *Androgynella* (synonymized with *Apseudes* by Larsen *et al*. (2011)). The morphological comparisons in Table 2 revealed no consistent diagnostic characters of *Muramurina* and *Androgynella* that could consistently separate them from *Apseudes*. *Androgynella* is thus confirmed as a junior synonym and *Muramurina* is here also suggested to be a junior synonym of *Apseudes*.

Family Neotanaidae (Article 5)

Neotanaidae is known to be an exclusively deep-sea family. At family level, these taxa are relatively easy to recognize by their comparative large size, uniramous but multi-articulated antennae, and their long uropods (Larsen & Blazewicz-

Paszkwycz 2003). This family is represented in this thesis by the species: *Neotanais bicornutus* and *Venusticurs thor* **(Article 5).**

Before Larsen (1999) transferred *Neotanais insolitus* (Gardiner, 1975) to *Venusticrus*, this genus was only represented by *V. glandurus* (Gardiner, 1975). Larsen (1999: 1118) justified this change because *Venusticrus* had the uropod attachment on the ventral surface instead of on the lateral margins as in all other species of *Neotanais*. In the present thesis, the morphological observations of specimens of *V. thor* strongly support transfer the species *V. glandurus* to *Venusticrus*. Additionally, a consistent difference was observed between *Venusticrus* and the other genera of Neotanaidae, i.e. *Neotanais*, *Herpotanais* and *Carololangia,* regarding the armament at the dactylus of pereopods 4–6. These last three genera, or at least in the species that are properly described and illustrated, have a dactylus with a row of denticles arranged as a ring around the insertion of unguis (Figure 35D–F). In *Venusticrus*, the species have the previously-mentioned dactylus armament consisting of bilobate and finely serrated terminal shields at the insertion of the unguis (Figure 38J–L). Until now, this character has not been used for genus separation, but the results in this thesis indicate that it might be a potential generic character, which is very conservative and easy to observe. This character should thus be considered for further morphological analyses. Regarding the ventral uropod attachment, this character is found exclusively in the species of *Venusticrus*, possibly being an apomorphic character of this genus, while in *Neotanais*, *Herpotanais and Carololangia* the uropod is laterally attached. Together with the characters described by Gardiner (1975) and new characters cited above, a new diagnosis for *Venusticrus* is proposed here (Chapter II, **Article 5**). This allowed for the transfer of the Atlantic species *N. rotermundiae* to *V. rotermundiae* (new combination) (Weigmann & Guerrero-Kommritz, 2009).

Finally, morphological comparisons of species that closely resemble *V. thor* and *N. bicornutus* are discussed in detail in the Chapter II (**Article 5**).

Family Akanthophoreidae (Article 6)

Before being raised to family rank, several phylogenetic analyses have been performed for the family Akanthophoreidae, but all failed to resolve its systematics (Larsen & Wilson 2002; Guerrero-Kommritz & Brandt 2005; Bird & Larsen 2009).

In the present thesis, a phylogenetic revision of this family based on morphological data was provided (**Article 6**). In addition, we also list several new morphological characters for this family. Herein, Akanthophoreidae is confirmed as monophyletic (Figure 39). This result agrees with what was suggested by Błażewicz-Paszkowycz & Bamber (2011), whom assigned the type-genus *Akanthophoreus* Sieg, 1986 to family Akanthophoreidae. However, these authors did not present a phylogeny analyses to confirm that. The monotypic genus *Gejavis,* previously assigned to Akanthophoreidae by Błażewicz-Paszkowycz & Bamber (2012), is herein relocated to *incertae sedis*, since it does not correspond to the family diagnosis. Moreover, three new species and one new genus are described from the Akanthophoreidae (i.e. *Chauliopleona ciimari*, *C. andeepi* and *Parakanthophoreus greenwichius*) (Figures 40, 43 and 46, respectively). The genus *Parakanthophoreus* is herein erected to accommodate some of the *Akanthophoreus* species previously synonymized with *Paraleptognathia* by Guerrero-Kommritz & Brandt (2005). However, this synonymization was not accepted by Bird (2007) as no synapomorphies were assigned to this genus. Additional information of the Akanthophoreidae is discussed in the remarks section (Chapter II, **Article 6,** p. 187–189).

4.4. Morphological phylogeny

In order to evaluate the phylogenetic relationships between the families studied in Chapter II (i.e. Colletteidae, Akanthophoreidae, Paratanaidae, Leptocheliidae, Neotanaidae and Apseudidae) we performed additional analyses, using at least one genus per family in the character matrix (Appendix VII). We also included as many *incertae sedis* genera as possible in order to make the analyses as comprehensive as possible. The morphological data was generated through phylogenetic analyses using Bayesian Inference (BI) and Maximum Parsimony (MP) methods. The characters descriptions and methodology follow the same used for the species used in the Chapter III (**Article 7** [Morphological phylogenetic analyses section] and Appendix II).

Overall, the phylogenetic relationships in BI and MP analyses recovered clades with high support values of posterior probabilities and bootstraps (>70 and >50, respectively). A brief discussion is here presented only regarding the clades encompassed by the families Colletteidae, Akanthophoreidae, Paratanaidae, Leptocheliidae, Neotanaidae and Apseudidae (Figure 54A, B).

The family Colletteidae is represented by four genera: *Collettea, Cheliasetosatanais, Leptognathiella* and *Caudalonga*. Both phylogenetic analyses showed this family as polyphyletic inside Clade I (Figure 54A, B). Curiously, in the BI phylogenetic analyses the type-genus *Collettea* appeared related with support (>71) with the *incertae sedis* genus *Armaturatanais* (Figure 54A). The relationships among the remaining genera of Colletteidae studied in the present thesis is further discussed in the heading 4.5.

The monophyly of family Akanthophoreidae was tested and confirmed using MP analyses in Chapter II (**Article 6,** Figure 39). Herein, this family was represented by three genera: *Chauliopleona, Parakanthophoreus* and *Stenotanais*. Here, the morphological phylogenetic analyses of the BI and MP (Figure 54A, B) grouped the Akanthophoreidae genera differently from the previous revision (**Article 6**, Figure 39). While in both BI and MP analyses *Stenotanais* did not group with the other Akanthophoreidae genera (Figure 54A, B), in the previous analyses this genus clustered inside Akanthophoreidae (**Article 6**, Figure 39). As in the current MP analysis we add several new characters, as well as different taxa from the previous MP analysis (**Article 6,** Figure 39), these could be the reasons for the different topologies. This clade do not identify any synapormophies, but it is grouped by the article 2 of the maxilliped palp presenting bifid/trifid/strongly pectinate spiniform seta; mandible molar presenting acuminate/armed shape.

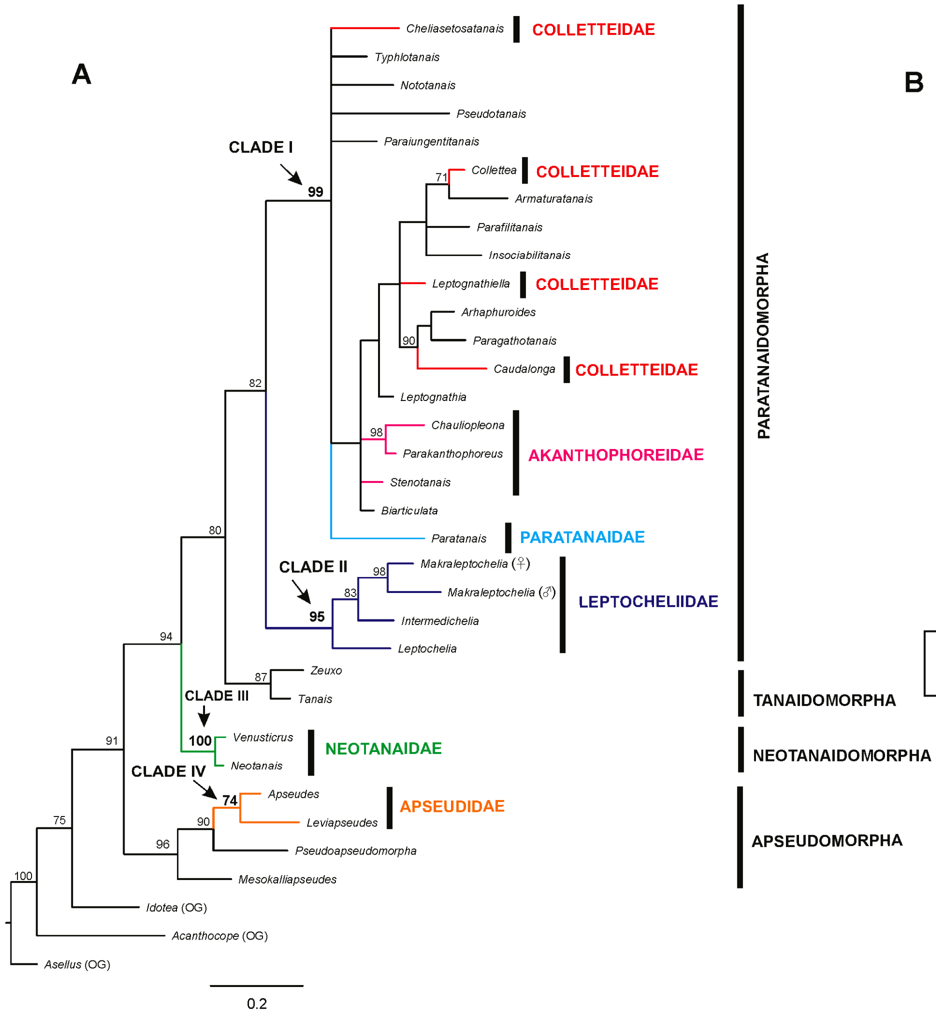
The family Paratanaidae is considered one of the few families among Tanaidacea that has remained stable since its establishment, and it is probably the only one which is uncontroversial (Bird & Larsen 2009). In the present analyses, this family was only represented by its type-genus *Paratanais* that clustered within Clade I (Figure 54A). This Clade also includes specimens from Akanthophoreidae and Colletteidae families among others. In the MP analyses, this Clade is supported by one synapomorphy: the fusioned maxilliped basis (Figure 54B). Due to this character, Paratanaidae seems to be more related to Akanthophoreidae than to any of the other analyzed families, i.e. Leptocheliidae, Apseudidae, Neotanaidae and Colletteidae (Figure 54A, B).

All analyzed genera from the family Leptocheliidae appeared grouped in a single Clade (Clade II, Figure 54A, B) with high support in both phylogenetic analyses (BI >95 and MP >73). In the MP analyses, the Leptocheliidae was not supported by any synapomorphy. However, its genera were grouped by the following characters: the presence of two pairs of labial lobes; the pereopod 1 with dactylus or unguis clearly longer than propodus (except for the male of *Makraleptochelia*); the pereopods 2–3 carpus ventrodistal spiniform setae absent (except for some species of *Leptochelia*); the pereopods 4–6 basis stout (≤ 2.5 times longer than broad); the pereopods 4–6 carpus with two or three spiniform setae. Both phylogenetic trees showed Leptocheliidae (Clade II) as sister-taxa of the large Clade I forming the suborder Paratanaidomorpha. Finally, both phylogenetic analyses (BI and MP) here support our changes for this family presented in the Chapter II, **Article 2**. These include 1) to restore the genus *Intermedichelia* and 2) to confirm *Makraleptochelia* for this family (Figure 54A, B).

The family Neotanaidae was represented by its type-genus *Neotanais* and *Venusticrus*. These grouped in a single Clade (Clade III) with support in both BI and MP phylogenetic analyses (100/97) (Figure 54A, B). Among the families discussed here, Neotanaidae was one of the families forming a Clade with high support values for BI and MP. In the MP analyses, the Neotanaidae was not supported by a single synapomorphy. However, its genera were grouped by twelve characters.

Finally, the family Apseudidae was also represented by its type-genus *Apseudes* and one deep-sea genus *Leviapseudes*. In both BI and MP phylogenetic analyses (74/51) (Figure 54A, B) these genera grouped together inside the Apseudomorpha. With this dataset, Apseudidae appears with support in MP analysis and presented three synapomorphies: cephalotorax with ventral hyposphenian/sternal spur; pereopod 1 with spiniform coxa; and, pereopod 1 with exopod.

In conclusion, the families Leptocheliidae, Neotanaidae and Apseudidae are monophyletic, while Akanthophoreidae and Colletteidae are not. In addition, the large Clade I formed by Akanthophoreidae, Colletteidae and Paratanaidae was grouped by one synapomorphy, while Clade IV (i.e. Apseudidae) was grouped by three synapomorphies.



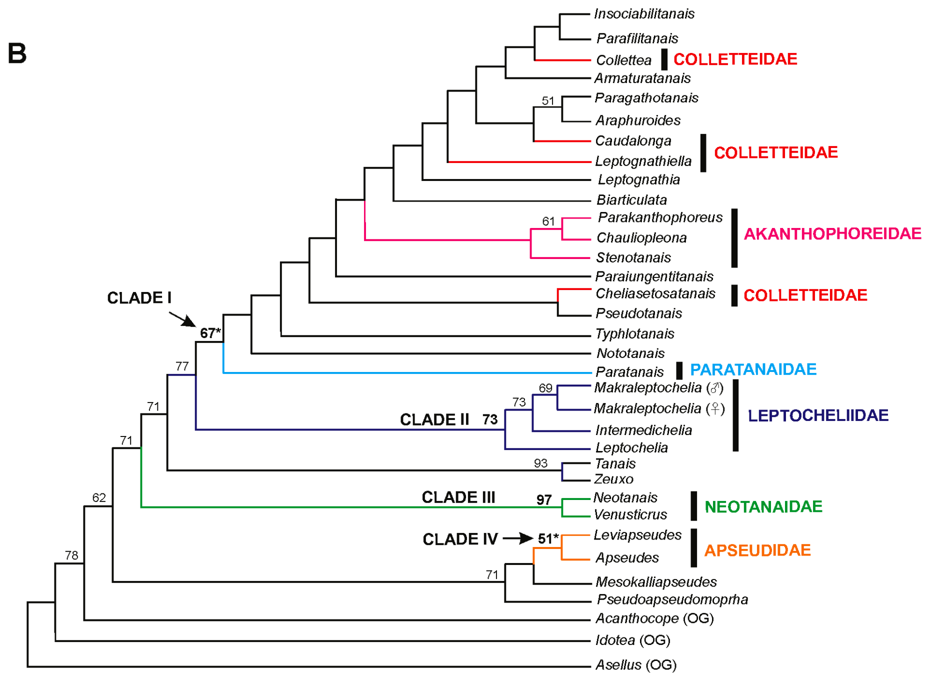


Figure 54. (A-B) Morphological phylogenetic trees obtained by the BI and MP methods, respectively, using Isopoda as outgroups. Tree topologies from BI and MP support values above nodes >70 and >50 are given, respectively. **(B)** Maximum Parsimony (MP) resulted from four trees from the matrix shown in Appendix VII. Support values with asterisk presented at least one synapomorphy (see text). Bold and colored taxa names in upper case labelling sidebars indicate the suborders and families of Tanaidacea discussed herein, respectively.

4.5. Systematics changes based on combined morphological and molecular data

Morphological approaches are undoubtedly the most common among the researchers when dealing with Tanaidacea, while studies using molecular data are still rare. Indeed, in the few studies published until now for this group, only Drumm (2010) and Kakui *et al.* (2011) performed molecular phylogenetic analyses, using three genes or one, respectively. Futhermore, the combination of both morphological and molecular data has never been applied to the Tanaidacea at all. This thesis is the first to propose a comprehensive phylogeny based on this combination.

The systematics of Tanaidacea was firstly designed by Lang (1949) divided the order into two suborders: Monokophora and Dikonophora. Later, Sieg (1980), based on morphological characters, renamed Monokophora as Apseudomorpha, while Dikonophora was separated into two suborders - Tanaidomorpha and Neotanaidomorpha. More recently, the systematics of Tanaidacea changed based on the results obtained by the exclusively use of molecular data (Kakui *et al*. 2011). These authors suggested a new classification for the Tanaidacea, because the former suborder Neotanaidomorpha grouped with superfamily Tanaoidea. Thus, they demoted Neotanaidomorpha to a superfamily rank (i.e. Neotanaoidea) and included it in the Tanaidomorpha (Kakui *et al*. 2011). As consequence changing the systematics from three suborders into two.

In the present thesis, this classification was challenged, and the monophyletic status of these suborders was tested. For that, we analyzed 45 combined sequences of three different genes (i.e. mtDNA COI, 28S and H3) and a total of 112 morphological characters (ten were added from the description of the eleven new species described in the Chapter II [**Articles 1–6]**). The obtained phylogenetic analyses permitted for a revision of the systematics of Tanaidacea and propose a new classification (Chapter III, **Article 7**).

Overall, the molecular phylogenetic trees (Figure 50) showed a better resolution than the morphological trees (Figure 49). More, the combination of both data sets (morphological and molecular) presented a significant increase on the resolution of the phylogeny (Figure 51). This combination, which has never previously been used in Tanaidacea before, confirmed the monophyly of all superfamilies (i.e. Paratanaoidea, Tanaoidea, Neotanaoidea and Apseudoidea). As a consequence of the position of Paratanaoidea (see below) we are now changing the systematics to include four suborders rather than two (Chapter III, **Article 7,** Figure 52).

The position of superfamily Neotanaoidea suggests that the Neotanaidomorpha should be re-erected to suborder. This is also supported by their life history traits, e.g., neotanaids are free-living surface dwellers (Gardiner 1975), contrary to tanaidomorphans which are mostly, if not exclusively, tube dwellers (Holdich & Jones 1983). Additionally, as Tanaoidea appears to be closer related to Neotanaoidea than to Paratanaoidea, we herein suggest to elevate both former tanaidomorphan superfamilies to suborder rank as Tanaidomorpha and Paratanaidomorpha (new suborder), respectively (Chapter III, **Article 7,** Figure 52). Moreover, and despite the relative high level of homoplasy index (HI= 0.6023) found, all suborders were supported for at least one synapormorphy (Chapter III, **Article 7,** Figure 51B).

Therefore, despite our tree topology (regarding suborders level) being similar to that proposed by Kakui *et al*. (2011), it also considers the morphological differences (and similarities) among the suborders discussed in this thesis. In addition, the history traits of both Neotanaidomorpha and Paratanaidomorpha (as cited above) are taken into account.

In conclusion, including the re-erected Neotanaidomorpha, the Tanaidacea systematics now consists of four extant suborders. This new suborder arrangement is supported by all analyses performed herein, whether being done when using the single morphological- or molecular- or by the combined phylogenetic analyses.

Family Colletteidae (Article 7)

No one disputes that the diagnosis of Colletteidae is too extensive and that the family is not monophyletic (Larsen & Araújo-Silva 2014a). In the present thesis, this family´s placement was tested through combined morphological and molecular analyses. The analyses corroborated with this view and showed Colletteidae as polyphyletic. The type-genus *Collettea* and the recently genus *Cheliasetosatanais* were found in a separated clade to the other genera currently assigned to this family, i.e., *Caudalonga* and *Leptognathiella* (Figure 51A, B). Since *Collettea* is the type-genus we here suggested *Caudalonga* and *Leptognathiella* should be removed from Colletteidae. On the other hand, *Leptognathiella* appeared related to a well-supported clade formed by Akanthophoreidae and Leptognathiidae group, but is left as it is until new taxa should be included. Together with *Leptognathiella*, *Caudalonga* also appeared related to the Akanthophoreidae and Leptognathiidae group in the combined molecular phylogenetic analyses, but with relatively low support.

Larsen (2005) when describing *Caudalonga* observed that this genus shared a number of morphological characters with the families Akanthophoreidae and Colletteidae, but decided to assign this genus to Colletteidae. Thus, because the generic diagnosis of *Caudalonga* is clearly confusing, and because only a limited number of Akanthophoreidae taxa were used herein, we have abstained to include this genus in the Akanthophoreidae, but instead transferring it to *incertae sedis*.

Family Akanthophoreidae (Article 7)

Previous studies have claimed that the families Akanthophoreidae and Leptognathiidae Sieg, 1976 are closely related (Bird 2007; Larsen & Shimomura 2007). Therefore, it is possible that some species of Leptognathiidae genus (i.e. *Biarticulata*) should be transferred to Akanthophoreidae. This assumption is supported based on the phylogenetic analyses from the combined morphological and molecular dataset performed in this thesis (see Chapter III, **Article 7,** Figure 51A, B). These analyses showed a clade formed by *Chauliopleona, Biarticulata, Leptognathiella* and *Stenotanais*. However, because of the current systematics problems with the family Leptognathiidae and because of the few taxa examined, we abstain from making changes for now.

Family Typhlotanaidae (Article 7)

Regarding the genus *Insociabilitanais*, Larsen (2005) placed it as *incertae sedis*. This author described this genus as sharing morphological characters with taxa from several families (e.g. Typhlotanaidae, Agathotanaidae, Colletteidae). In the present thesis, *Insociabilitanais* was found grouping with *Typhlotanais* (Figures 50 and 51A) with high support values. In addition, despite this arrangement was not seen in the morphological phylogeny (Figure 49A, B), *Insociabilitanais* share characters with Typhlotanaidae by the following characters: uropods, general morphology of the mouthparts, and chelipeds among other characters. Therefore, it is suggested that *Insociabilitanais* should be transferred to the Typhlotanaidae.

Genus *Paraiungentitanais* (Article 7)

In the present thesis, the families Cryptocopidae and Leptocheliidae are represented by the genera *Paraiungentitanais* and *Leptochelia*, respectively. The family Cryptocopidae was erected by McLelland (2008), later confirmed by Bird & Larsen (2009), and contains taxa mostly found in deep-sea environments. In contrast, Leptocheliidae is a family that occurs almost exclusively in shallow-water habitats (except for genera *Bathyleptochelia* and *Mesotanais*) (Edgar 2012). In the present thesis, except for the morphological phylogenetic analyses (Chapter III, **Article 7**, Figure 49), *Paraiungentitanais* and *Leptochelia*, always cluster together in a well supported clade (Figures 50 and 51A). This suggests that the *Paraiungentitanais* could be included in family Leptocheliidae. Regarding the morphological phylogeny, this separation as well as in other phylogenetic analyses (e.g. Larsen & Wilson 2002) could be explained by the still too incomplete description of *Paraiungentitanais*. This genus was abstained from Bird & Larsen (2009), due to the lack of characters to fill the matrix. While in the molecular approach the information is much more precise. In this thesis, only few specimens of *Paraiungentitanais* were found and most were used for molecular purpose. Thus, since this association is still new, we here refrain to transfer this genus for Leptocheliidae until new representatives should be included.

4.6. The phylogenetic position of Tanaidacea within the Peracarida

An interesting pattern regarding the phylogenetic position of Tanaidacea within superorder Peracarida emerged when the suborders Apseudomorpha, Neotanaidomorpha and Tanaidomorpha appeared clustering with Isopoda. These phylogenetic analyses were based solely in a multigene molecular approach, thus not including morphological data. These analyses were generated using the Bayesian Inference (BI) and Maximum Likelihood (ML) methods, following the methodologies described in Chapter III (**Article 7,** [Molecular phylogenetic analyses]). The final molecular dataset (28S+COI+H3) included 32 sequences (1453 bp), 24 Tanaidacea, four Isopoda, one Cumacea, Amphipoda, Mysida and Decapoda.

A single congruent tree was recovered by both approaches, revealing the same topology and is show in Figure 55. Five major clades were retrieved (Clades I-V) all presenting high supported values of posterior probabilities and bootstraps (>80 and 70, respectively).

The 'mancoid hypothesis'

Over the last decades several molecular studies concerning the Peracarida have been performed (e.g. Spears *et al*. 2005; Jenner *et al*. 2009). In most of those studies Isopoda and Cumacea are regularly grouped as sister-taxa to the Tanaidacea, like in earlier morphological phylogenies. After a broad morphological study of Peracarida, Watling (1981) found that Tanaidacea, Cumacea, Spelaeogriphacea and Isopoda grouped together (Figure 56). Based on that, this author raised a hypothesis he called the 'mancoid' taxa lineage (taxa lacking the posterior legs in their first postmarsupial stage) that represents a clade formed by Tanaidacea+Cumacea+Spelaeogriphacea+Isopoda. Other authors, based on morphological phylogenies, have also suggested those orders closely related (e.g. Pires 1987) and so have others based on molecular phylogenies (e.g. Spears *et al*. 2005). One molecular study, however, found some tanaid taxa clustering within the Isopoda, thus suggesting a big monophyly problem (e.g. Wilson 2009: 186; fig. 2) (Figure 56).

In the present thesis, we tested the monophyly of Tanaidacea by including several other Peracarida (i.e. Isopoda, Cumacea, Amphipoda and Mysida) and decapod taxa as outgroups. Our results confirmed that a triad clade was formed, supporting a "mancoid lineage" (i.e. Cumacea, Tanaidacea and Isopoda) as suggested by Watling (1981). Our results found the Mysida and Amphipoda as sister-orders. The "mancoid lineage” is also, according to Richter & Scholtz (2001), supported by the characters of a dorsally folded embryo, the manca stage, and by the formation of the mid-gut.

As previously found by Wilson (2009), our phylogenetic analyses also showed Isopoda clustering as sister-clade with Tanaidacea suborders Apseudomorpha, Neotanaidomorpha, and Tanaidomorpha, but not with

Paratanaidomorpha (Figure 55, represented by Clades II-V). A similar result was also reported in the molecular phylogeny performed by Drumm (2010: 696). This author found that the isopods *Sphaeroma terebrans* and *Asellus aquaticus* grouped within the tanaidaceans when they were used as additional outgroups. However, this author did not specify within which tanaid suborders. It is also important to notice that this clustering has until now only been reported in molecular phylogenies, not in morphological phylogenies. Sieg (1983) described a hypothetic ancient Tanaidacea with biramous antennules with a four-articulated peduncle, which is a known plesiomorphic character also found in several Isopoda genera (e.g. *Asellus*, *Synassellus*, *Jaera*, *Eurydice*, *Sphaeroma*). This author suggested that this character would be a synapomorphy of Tanaidacea and Isopoda. Sieg (1983) also suggested that the character of fusion of all pleonites and telson could be such a synapomorphy. However, this character is only found in some species of some tanaid families, e.g., Anarthruridae (females of *Anarthrura simplex* G.O. Sars, 1882) and Metapseudidae (genus *Cryptapseudes*).

The result of our analyses (Figure 55) confirmed Kakui *et al*. (2011) finding of a close relationship between superfamilies Tanaoidea and Neotanaoidea (Figure 55, Clades II and III) However, when including other peracarids as outgroups, surprisingly the molecular phylogenetic analyses (BI and ML), showed the suborders Neotanaidomorpha and Tanaidomorpha as sister-clade to the suborder Apseudomorpha rather than to Paratanaidomorpha (Figure 55, Clades II-IV). This contradicts what was presented by Kakui *et al*. (2011) (Figure 4). In addition, these results supports the new division of suborder classification proposed in this thesis (Chapter III, **Article 7**), as Neotanaidomorpha and Tanaidomorpha seemed to be indeed closer related to Apseudomorpha than to Paratanaidomorpha.

The morphological evidence also supports a close relationship between Neotanaidomorpha and Apseudomorpha (Lang 1956; Sieg 1988). Lang (1956) stated that Neotanaidae shared many characters with Apseudomorpha. Nevertheless, in this same study Lang also listed other characters that family Neotanaidae also shares with Tanaidomorpha. Lang (1956) finally concluded that this taxon could represent a linkage between the Apseudomorpha and Tanaidomorpha. Sieg (1988), also using a morphological phylogenies, supported

Lang´s statement of Apseudomorpha and Neotanaidomorpha being closely related (Figure 4).

By all said above, it is obvious that further studies are needed concerning the intermingled relation between Tanaidacea and Isopoda. These should include more gene sequences and morphological characters for both taxa. Because the main goal in this thesis was the internal relationships in the Tanaidacea, this linkage with the Isopoda is for now put aside.

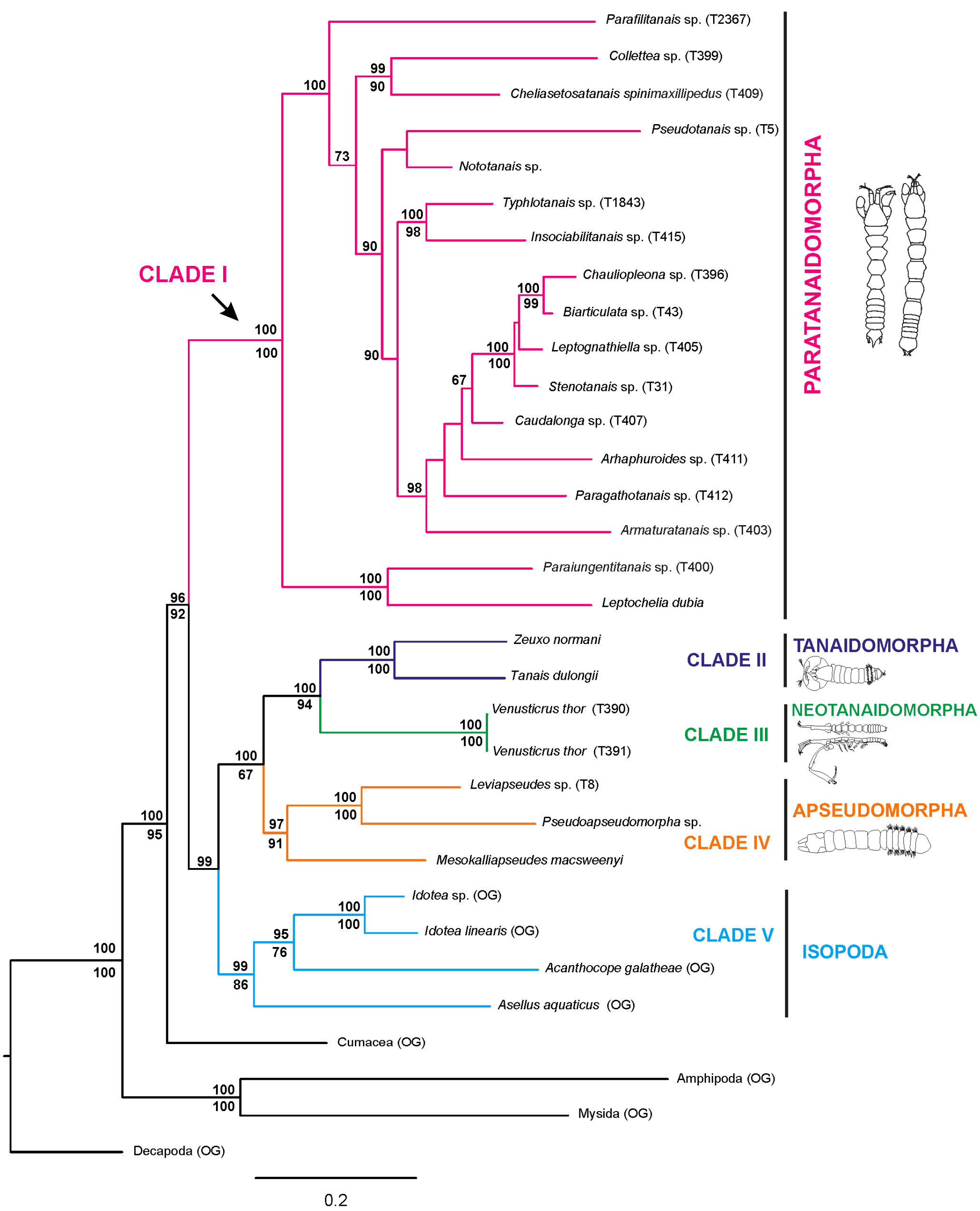


Figure 55. Phylogenetic tree obtained by the Bayesian Inference analysis (BI) of the molecular combined dataset (COI+H3+28S; 1453 bp) of Tanaidacea using Isopoda, Cumacea, Amphipoda, Mysida and Decapoda as outgroups. The tree topologies resulting from ML and BI approaches were congruent; only support values >70 are given, as Bayesian posterior probability (BI) above nodes and bootstrap support (ML) below nodes. Colored taxa names in upper case labeling sidebars indicate the suborders of Tanaidacea discussed in this work; except for the blue taxa, which corresponds to the order Isopoda (outgroup). Pictured are the female and male of *Cheliasetosatanais spinimaxillupedus* modified from Larsen & Araújo-Silva (2014a: 3-4); followed by *Tanais dulongii* (Audouin, 1826), modified from Edgar (2008:7); male habitus of *Venusticrus thor* Araújo-Silva *et a*l. (2015: 548) and female of *Mesokalliapseudes macsweenyi* modified from Drumm (2003:3).

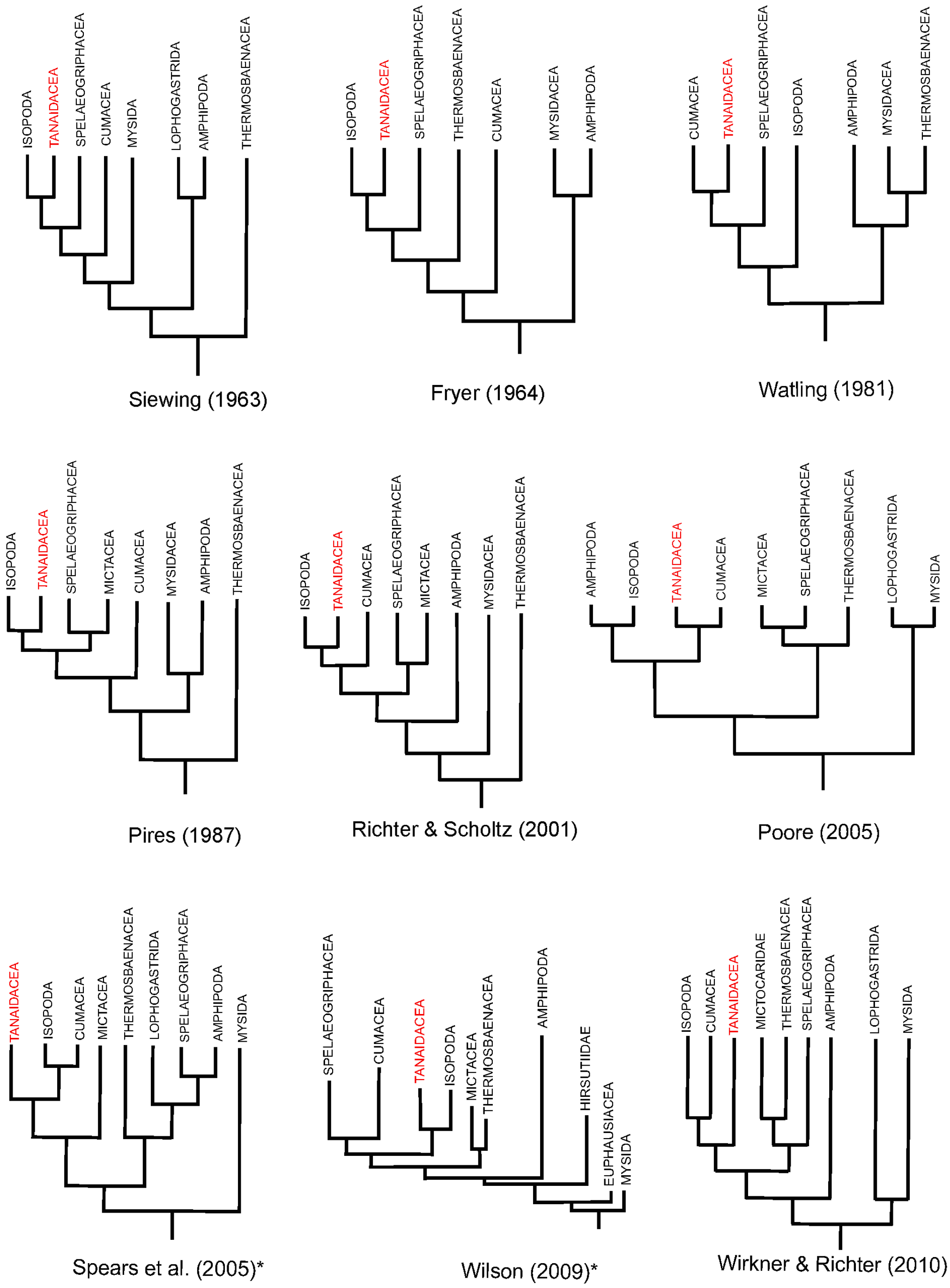


Figure 56. Nine alternative phylogenetic hypotheses for extant Peracarida orders. Drawings modified from: Siewing (1963); Fryer (1964); Watling (1981); Pires (1987); Richter & Scholtz (2001); Poore (2005); Spears *et al*. (2005); Wilson (2009); and Wirkner & Richter (2010). *Drawings with asterisk were based on molecular phylogeny only.

4.7. Future perspectives

In this thesis, many issues regarding the systematics, morphology and molecular phylogenies of the Tanaidacea were answered. However, the phylogenetic results showed some relationships that still need further clarifications.

Paraiungentitanais - Leptochelia

The clade formed by the families Cryptocopidae and Leptocheliidae were represented by the genus *Paraiungentitanais* and the genus *Leptochelia*, respectively. This association raises the question if *Paraiungentitanais* should be transferred to family Leptocheliidae. Herein we abstained to make this change, since *Paraiungentitanais* is only recorded in the deep-sea, contrarily to *Leptochelia*. Additionally, the *Paraiungentitanais* description is very incomplete (Sieg 1977). Thus, in order to confirm this association, a re-description of *Paraiungentitanais* is needed (Araújo-Silva *et al*. research in progress) as well as the inclusion of other representatives from both families in the analyses.

Leptocheliidae

In all phylogenetic analyses, this family appeared always separated of the big Clade formed by the deep-sea genera. It is possible that within the new suborder Paratanaidomorha, Leptocheliidae can be raised to a superfamily rank. However, since this family is extremely heterogeneous and widely distributed, thus to confirm this assumption much more representatives from other genera should be included.

Akanthophoreidae - Colletteidae - Leptognathiidae

The clade formed by these three families confirms the close relationships among them. It is possible that some species of Leptognathiidae as well as some species of the apparent polyphyletic Colletteidae (e.g. *Leptognathiella*) would be transferred to Akanthophoreidae (e.g. *Biarticulata*) when more representatives from each of these families are included. In this scenario two different subfamilies could be erected. As only a few representatives were collected during this thesis, this issue cannot be answered. Including more representatives of these families should allow defining them in the future.

Incertae sedis genera

Caudalonga was here transferred from Colletteidae (polyphyletic family) to *incertae sedis*, since it did not cluster inside Colletteidae or in any family in the phylogenetic analyses. Despite being well described, this genus is monotypic and descriptions of new species and inclusion of more families should allow to place it in the systematics.

Isopoda and Tanaidacea

An interesting relationship between Isopoda and Tanaidacea is found in our phylogeny questioning the position of Tanaidacea within the Peracarida. When adding other Peracarida (e.g. Cumacea, Amphipoda, Mysida) and Decapoda as outgroup, the analyses showed some Isopoda clustering within Tanaidacea. This relationship was only observed using molecular data and not morphological. Therefore, we hope in the near future to also include morphological characters in order to combine both datasets. Collaborations with other peracarid specialists should be also considered in the future.

4.8. References

Anderson, G. (2013) Tanaidacea-Thirty Years of Scholarship (Vers. 1.0, May, 2013). Available from: http://peracarida.usm.edu/TanaidaceaText.htm (Accessed 14 January 2016)

Araújo-Silva, C.L. & Larsen, K. (2012a). Tanaidacea (Tanaidacea: Crustacea) from Brazil. IV. A new genus and two new species from the family Leptocheliidae. *Zootaxa*, 3523: 1–19.

Bamber, R.N. & Sheader, M. (2003). *A reinterpretation of the taxonomy and zoogeography of Pakistanapseudes and Swireapseudes (Crustacea: Tanaidacea)*: Hong Kong taxa in the world context. Pp. 167–194, *In:* Morton, B., (ed.), Perspectives on Marine Environment Change in Hong Kong and Southern China, 1977-2001. Proceedings of an International Workshop Reunion Conference, Hong Kong 21-26 October, 2001. Hong Kong, Hong Kong University Press.

Bird, G.J. (2007). *Families Anarthruridae Lang, 1971, Colletteidae Larsen & Wilson, 2002, and Leptognathiidae Sieg, 1976*. *In:* Larsen, K., & M. Shimomura (eds.), Tanaidacea (Crustacea: Peracarida) From Japan III. The Deep Trenches: The Kurile-Kamchatka Trench and Japan Trench. *Zootaxa*, 1599: 61–85.

Bird, G.J. (2011). Paratanaoidean tanaidaceans (Crustacea: Peracarida) from littoral and shallow sublittoral habitats in New Zealand, with descriptions of three new genera and seven new species. *Zootaxa*, 2891: 1–62.

Bird, G.J. & Larsen, K. (2009). Tanaidacean phylogeny - the second step: the basal paratanaoidean families (Crustacea: Malacostraca). *Arthropod Systematics and Phylogeny*, 67(2): 137–158.

Błażewicz-Paszkowycz, M. & Bamber, R.N. (2011). Tanaidomorph Tanaidacea (Crustacea: Peracarida) from mudvolcano and seep sites on the Norwegian Margin. *Zootaxa*, 3061: 1–35.

Błażewicz-Paszkowycz, M. & Bamber, R.N. (2012). The Shallow-water Tanaidacea (Arthropoda: Malacostraca: Peracarida) of the Bass Strait, Victoria, Australia (other than the Tanaidae). *Memoirs of Museum Victoria*, 69: 1–235.

Błażewicz-Paszkowycz, M., Jennings, R.N., Jeskulke, K. & Brix, S. (2014). Discovery of swimming males of Paratanaoidea (Tanaidacea). *Polish Polar Research,* 35 (2): 415–453.

Brandt, A. (1992). Origin of Antarctic Isopoda (Crustacea, Malacostraca). *Marine Biology*, 113: 415–423.

Drumm, D.T. (2010). Phylogenetic relationships of Tanaidacea (Eumalacostraca: Peracarida) inferred from three molecular loci. *Journal of Crustacean Biology*, 30 (4): 692–698.

Edgar, G. J. (2012). New Leptocheliidae (Crustacea: Tanaidacea: Tanaidomorpha) from Australian seagrass and macro-algal habitats, and a redescription of the poorly-known *Leptochelia ignota* from Sydney Harbour. *Zootaxa*, 3276: 1–37.

Feldmann, R. M. & Tshudy, D. M. (1989). *Evolutionary pattern in macrurous decapod crustaceans from Cretaceous to early Cenezoic rocks of the James Ross Island region, Antarctica*. Pp. 183–195. *In:* Crame, J.A. (ed.), Origin and evolution of the biosphere, Vol. 47. Geological Society Special Publications, London.

Gardiner, L.F. (1975). The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea). *Smithsonian Contributions to Zoology*, 170: 1–265.

Guerrero-Kommritz, J. & Brandt, A. (2005). Phylogenetic analysis of genera of 'Akanthophoreinae' (Crustacea: Tanaidacea). *Organisms, Diversity & Evolution*, 5 (4): 285–296.

Guţu, M. (1996). Tanaidaceans (Crustacea, Peracarida) from Brazil, with description of new taxa and systematical remarks on some families. *Travaux du Muséum National d´Histoire naturelle "Grigore Antipa",* 36: 23–133.

Guţu, M. (2006). *New Apseudomorph Taxa of the World Ocean: Crustacea, Tanaidacea*. Pp. 317. Curtea Veche, Bucharest, Romania.

Holdich, D.M. & Jones, J.A. (1983). The distribution and ecology of British shallow-water tanaid crustaceans (Peracarida, Tanaidacea). *Journal of Natural History*, 17 (2): 157–183.

Jenner, R.A., Dhubhghaill, C.N., Ferla, M.P. & Wills, M.A. (2009). Eumalacostracan phylogeny and total evidence: limitations of the usual suspects. *BMC Evolutionary Biology*, 9: 21. http://www.biomedcentral.com/1471-2148/9/21

Kakui, K. & Hiruta, C. (2013). Selfing in a malacostracan crustacean: why a tanaidacean but not decapods. *Naturwissenschaften (The Science of Nature)*, 100: 891–894. DOI 10.1007/s00114-013-1079-5

Kakui, K., Katoh, T., Hiruta, S.F., Kobayashi, N. & Kajihara, H. (2011). Molecular systematics of Tanaidacea (Crustacea: Peracarida) based on 18S sequence data, with an amendment of suborder/superfamily-level classification. *Zoological Science*, 28: 749–757.

Lang, K. (1949). Contribution to the systematics and synonymics of the Tanaidacea. *Arkiv för Zoologie, Series 1*, 42 (18): 1–14.

Lang, K. (1953). *Apseudes hermaphroditicus* n.sp. A hermaphroditic Tanaide from the Antarctic. *Arkiv för Zoologi, Series 2,* 4: 341–350 (plates I-IV).

Lang, K. (1956). Neotanaidae nov. fam., with some remarks on the phylogeny of the Tanaidacea. *Arkiv för Zoologi*, 9: 469–475.

Lang, K. (1971). Taxonomische und phylogenetische Untersuchungen über die Tanaidaceen. 6. Revision der Gattung *Paranarthrura* Hansen, 1913, und Aufstellung von zwei neuen Familien, vier neuen Gattungen und zwei neuen Arten. *Arkiv för Zoologi, Series 2*, 23: 361–401.

Larsen, K. (1999). Deep-sea tanaidaceans (Crustacea: Peracarida) from the Albatross cruises 1885-86, with keys to the suborder Neotanaidomorpha. *Journal of Natural History*, 33: 1107–1132.

Larsen, K. (2005). *Deep-Sea Tanaidacea (Peracarida) from the Gulf of Mexico*. Pp. 391. Brill, Leiden.

Larsen, K. & Araújo-Silva, C.L. (2014a). A new genus of Colletteidae (Crustacea: Peracarida: Tanaidacea) from the Pacific with comments on dimorphic males with species specific characters. *Journal of the Marine Biological Association of the United Kingdom*, 94 (5): 969–974. doi:10.1017/S0025315414000101

Larsen, K., & Błażewicz-Paszkowycz, M. (2003). A new species of *Neotanais* Beddard (Crustacea: Tanaidacea) from the Subantartctic [sic], off the Falkland Islands. *Zootaxa*, 339: 1–11.

Larsen, K. & Froufe, E. (2013). A new polymorphic species of *Leptochelia* (Crustacea: Tanaidacea) from Guinea Bissau, West Africa, with comments on genetic variation within *Leptochelia*. *African Invertebrates*, 54 (1): 105–125.

Larsen, K., & Shimomura, M. (2007). Tanaidacea (Crustacea: Peracarida) from Japan. II. Tanaidomorpha from the East China Sea, the West Pacific Ocean, and the Nansei Islands. *Zootaxa*, 1464: 1–43.

Larsen, K. & Wilson, G.D.F. (2002). Tanaidacean phylogeny, the first step: The superfamily Paratanaidoidea. *Journal of Zoological Systematics and Evolutionary Research*, 40 (4): 205–222.

Larsen, K., Bertocci, I. & Froufe, E. (2011). *Apseudes talpa* revisited (Crustacea; Tanaidacea). The impact on apseudidaen systematics. *Zootaxa*, 2886: 19–30.

Mclelland, J.A. (2008). *A systematic and taxonomic review of the family Pseudotanaidae (Crustacea: Peracarida: Tanaidacea) based primarily on morphometric cladistic analyses*. Ph.D. Dissertation, Coastal Sciences, University of Southern Mississippi.

Pires, A.M.S. (1987). *Potiicoara brasiliensis*: a new genus and species of Spelaeogriphacea (Crustacea: Peracarida) from Brazil with a phylogenetic analysis of the Peracarida. *Journal of Natural History*, 21: 225–238.

Poore, G.C.B. (2005). Peracarida: monophyly, relationships and evolutionary success. *Nauplius*, 1 (3): 1–27.

Richter, S. & Scholtz, G. (2001). Phylogenetic analysis of the Malacostraca (Crustacea). *Journal of Zoological Systematics and Evolutionary Research*, 39: 113–136.

Rumbold C.E, Obenat S.M, Spivak E.D. (2012). Life history of *Tanais dulongii* (Tanaidacea: Tanaidae) in an intertidal flat in the Southwestern Atlantic. *Journal of Crustacean Biology*, 32: 891–898. doi:10.1163/1937240X-00002094

Rumbold, C.E., Obenat, S.M., Leonardi, M. S. & Spivak, E. D. (2015): Intersex in the gonochoristic crustacean *Tanais dulongii* (Audouin, 1826) (Peracarida: Tanaidacea: Tanaididae): a comparison of external reproductive characteristics. *Journal of Natural History* 49 (13-14): 775–788. DOI: 10.1080/00222933.2014.981309

Sieg, J. (1976). Zum natürlichen System der Dikonophora Lang (Crustacea, Tanaidacea). *Zeitschrift für Zoologischer Systematik und Evolutionsforschung*, 14: 177–198.

Sieg, J. 1977. Taxonomische Monographie der familie Pseudotanaidae (Crustacea, Tanaidacea). *Mitteilungen aus dem Zoologischen Museum in Berlin*, 53: 1–109.

Sieg, J. (1980). Sind die Dikonophora eine polyphyletische Gruppe? *Zoologischer Anzieger*, 205 (5-6): 401–416.

Sieg, J. (1983). *Evolution of Tanaidacea*. Pp. 229–256. *In:* Schram, F.R. (ed.), Crustacean Phylogeny. A.A. Balkema, Rotterdam, The Netherlands.

Sieg, J. (1984). Fact documentation and literature database for the crustacean order Tanaidacea. *Systematics Association*, Special Volume 26: 125–136.

Sieg, J. (1986). *Distribution of the Tanaidacea: Synopsis of the known data and suggestions on possible distribution patterns*. Pp. 165–194, *In:* Gore, R.H. & Heck, K.L. (eds.), Crustacean Biogeography, Crustacean Issues 4. A.A. Balkema, Rotterdam, The Netherlands.

Sieg, J. (1988). Das phylogenetische System der Tanaidacea und die Frage nach Alter und Herkunft der Crustaceenfauna des antarktischen Festlandsockels [The phylogenetic system of the Tanaidacea and the question of age and origin of the crustacean fauna on the Antarctic shelf]. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, 26: 363–379.

Silva-Brum, I.N. (1973). Contribução ao conhecimento da fauna do Arquipélago de Abrolhos, Bahia, Brasil, Nº. 4. Crustacea - Tanaidacea. *Boletim do Museu de História Natural UFMG Zoologia*, 18: 1–25.

Spears, T., DeBry, R.W., Abele, L.G. & Chodyla, K. (2005). Peracarid monophyly and interordinal phylogeny inferred from nuclear small- subunit robosomal DNA sequences (Crustacea: Malacostraca: Peracarida). *Proceedings of the Biological Society of Washington,* 118 (1): 117–157.

Suárez-Morales, E., Heard, R.W., García-Madrigal, S., Oliva-Rivera, J.J. & Escobar-Briones, E. (2004). Pp 123, *Catálogo de los Tanaidáceos (Crustacea: Peracarida) del Caribe Mexicano*. Conacyt, Semarnat, & Ecosur, Mexico.

Vanhöffen, E. (1914). Die Isopoden der deutschen Südpolar-Expedition 1901–1903. *Deutsche Südpolar-Expedition 15*, (Zoologie 7): 447–598.

Watling, L. (1981). An alternative phylogeny of peracarid crustaceans. *Journal of Crustacean Biology*, 1 (2): 201–210.

Weigmann, S. & Guerrero-Kommritz, J. (2009). New species of *Neotanais* Beddard, 1886 (Crustacea, Tanaidacea) from the deep sea of the tropical and southern East Atlantic Ocean. *Zootaxa*, 1992: 20–36.

Wilson, G.D.F. (2009). The phylogenetic position of the Isopoda in the Peracarida (Crustacea: Malacostraca). *Arthropod Systematics and Phylogeny*, 67 (2): 159–198.

WoRMS (World Register of Marine Species). (2015). WoRMS taxon details. Available from: http://www.marinespecies.org/index.php (accessed 15 December 2015)

APPENDICES

Appendix I. Character matrix data corresponding to the morphological phylogenetic analyses presented in Chapter II, **Article 6** (Figure 39).

Taxa/Characters	0–9	10–19	20–29	30–39	40–49
Heterotanoididae	1000000000	000010010[01]	0000000110	00100000[23][23]	0120001010
Leptocheliidae	1000000000	0000101010	1011001010	0000000014	010100[01]010
Nototanaidae	1100000000	0000100011	0000100110	0000010144	00210[01]1110
Tanaissuidae	0100000000	0000100011	0000100[34]10	1[01]00011244	0020001100
Typhlotanaidae	0000010000	0000110011	0000100100	0001010144	1021001100
Paratanaidae	1000000000	100102[01]011	00[02]0101010	0000110044	1021101110
Pseudozeuxidae	1100000001	0000100111	0000000110	0000000024	0110000010
Teleotanaidae	1100000001	0000100111	0000000110	0000000024	0110000010
Cryptocopidae	0110010000	0001020011	0000000300	0000010044	0021001100
Pseudotanaidae	[01]111000000	0000000010	0[01]00100[234]01	110001[12][12]44	[01]0[23]10[01][12]100
Colletteidae	0000000000	0001021011	0000100200	0000010034	[01][01]30001110
Tanaellidae	0000000000	0001020011	0000100200	0000010034	1131001110
Leptognathiidae	0000000000	0001020011	0000100410	0000010034	[01][01]20001110
Tumidochelia	0000000000	0001020011	0000100300	0001010034	10[23]1011110
Paraleptognathia	0000000000	0001020011	0000100300	0001010034	1121011110
Parakanthophoreus	0000000000	0001020011	0000100300	0001010034	1121011110
Akanthophoreus	0000000000	0011020011	0000100300	0001010034	1121011110
Chauliopleona	0000000000	0101020011	0000100300	0001010034	1121011110
Mimicarhaphura	0000000000	0001020011	0000100300	0001010034	1121011110
Anarthruridae	0000000[01]0[01]	0001030011	0000100500	0000010034	0130001101
Agathotanaidae	0000100010	000[01]010020	0000110[45]00	0000010034	0020001100
Mirandotanaidae	0000001000	0001020010	0000000500	1001010034	0030002110
Gejavis	0000000000	0001000111	0000100310	?000010133	2030001110
Stenotanais	0000000000	0001220011	0000100300	0001010034	1121011110

……continued on the next page

Appendix I. Character matrix (Chapter II, **Article 6**).

Taxa/Characters	50–59	0–69	0–79	80–89	90–99	100–102
Heterotanoididae	1000000001	2010000000	01000[01]0110	0010100010	00[01]100200	110
Leptocheliidae	100000100[01]	101[01]021000	1200011110	00[012]0000010	1001[01]00[12]00	[01]10
Nototanaidae	1000000012	3010110010	2210000[13]01	003030001[01]	0001200[12]10	110
Tanaissuidae	1010000[01]12	30101[12]0110	220000010[01]	0030310010	0001200210	110
Typhlotanaidae	0000000011	3000100000	1200011130	20[04]1310010	0001200211	110
Paratanaidae	1000001012	30101[12]1000	2100001220	1031310010	0001200[12]10	110
Pseudozeuxidae	1000000011	3010010000	1101010100	0020210010	1??0200210	100
Teleotanaidae	1000000011	3010010000	1101010100	0020210010	1??0200210	100
Cryptocopidae	0000000012	3010100000	1100000100	002031000[01]	0100200[12]10	1?0
Pseudotanaidae	1000010012	3010101001	22[02]00[01]0100	011[01]320010	0110[23]00[12]11	110
Colletteidae	100000001[23]	30200001[01]0	1210100100	0020310000	0000200110	00[01]
Tanaellidae	1000000012	3020000110	2210000301	0020310100	0111[32][01]0010	200
Leptognathiidae	10000[01]0013	3010101100	1210000201	0010[23]10000	0000200[12][01][01]	[01]10
Tumidochelia	000000001[12]	3120001110	2220000301	0020311100	0001200201	0?1
Paraleptognathia	010110001[12]	3120001110	2220000301	0020311100	0001200201	010
Parakanthophoreus	0[01]00000[01]1[12]	3120001110	2220000301	0020311100	0001200201	010
Akanthophoreus	000000011[12]	3120001110	2220000301	0020311100	0001200201	010
Chauliopleona	0[01]00000[01]1[12]	3120001110	2220000301	0020311100	0001200201	010
Mimicarhaphura	0100000011	3120001110	2220000301	0020311100	0001201201	0?0
Anarthruridae	0000000012	3010100000	1110000100	0020310000	0110[23]20010	210
Agathotanaidae	0000000013	3110100010	2110100100	0020300000	0111[234][01]0010	200
Mirandotanaidae	100000002[23]	3010100000	0102000200	2010330001	0111200110	000
Gejavis	1000000111	3021111010	212?010301	0030310000	0001200101	1?0
Stenotanais	0000000112	3120001110	2220020301	0020311100	0001200[12]01	0?[01]

Appendix II. Character descriptions corresponding to the morphological phylogenetic analyses presented in the Chapter III, **Article 7** (Figures 49 and 51) and in the Chapter IV, heading 4.4 (Figure 54).

1 Antenna article 2 thicker or longer than article 3 (0 = absent, 1 = present). This character corresponds to character ‘27’ from Bird & Larsen (2009).

2 Cheliped carpus distal margins extended as a ‘shield’ overlapping propodus (0 = absent, 1 = present). This character occurs in some species of Akanthophoreidae (e.g. *Chauliopleona andeepi* and *Parakanthophoreus greenwichius* Larsen & Araújo-Silva, 2014). It is not to be confused with character '58' that the ventral margin in the cheliped carpus is more pronounced than that of the dorsal margin.

3 Cheliped, male fixed finger reduced (0 = absent, 1 = present). This character is found mainly in some genera of family Leptocheliidae (e.g. *Makraleptochelia*).

4 Pereonite 3 with midlateral prolongation (0 = absent, 1 = present). This character was found in the genus *Intermedichelia* (family Leptocheliidae), but here was also found in genus *Paraiungentitanais* (Cryptocopidae). Although the morphological analysis did not show both genera together, the molecular and combined (Figure 50 and 53) analyses did place both families clustered. This grouping must be verified in the near future with description of new species found.

5 Pereopods 4–5 propodus with one long modified dorsodistal seta (0 = absent, 1 = present). This character corresponds to character ‘94’ from Bird & Larsen (2009). This character was scored by these authors to define the genus *Intermedichelia*, but is here also found in *Pseudotanais*.

6 Cephalotorax with ventral hyposphenian/sternal spur (0 = absent, 1 = present). This character here defines the family Apseudidae.

7 All pleonites with ventral keel/spurs (0 = absent, 1 = present). This character despite to be homoplastic and polymorphic is found in most species of the suborder Neotanaidomorpha and some of Paratanaidomorpha.

8 Antennule biramous or uniramous (0 = biramous, 1 = uniramous). This character defines the suborder Apseudomorpha.

9 Antenna biramous or uniramous (0 = biramous, 1 = uniramous). This character defines the suborder Apseudomorpha.

10 Antenna article 2 ventral acute spines/apophysis (0 = absent, 1 = present). This character despite polymorphic is found in many genera of Apseudomorpha and Leptocheliidae. Here was also found in the outgroup *Acanthocope*.

11 Maxilliped palp article 1 inner seta (0 = absent, 1 = present). This is a novel character for a phylogenetic study, here was found stable in Apseudomorpha, the genera *Zeuxo* and *Arhaphuroides*. Despite homoplastic may contain important phylogenetic information.

12 Maxilliped palp article 1 outer lateral simple seta (0 = absent, 1 = present). Similarly to character '11' this character is a novel, and despite seems fragile should be observed in the future.

13 Maxilliped palp article 2 outer lateral spiniform seta (0 = absent, 1 = present). This character is found mainly in apseudomorphans.

14 Maxilliped palp article 2 outer lateral simple seta (0 = absent, 1 = present). See character '12'.

15 Cheliped merus ventral setae count (0 = four or more, 1 = three, 2 = two, 3 = one; 4 = absent). This character corresponds to character ‘68’ from Bird & Larsen (2009).

16 Cheliped merus ventral setae type (0 = absent; 1 = simple; 2 = plumose). This character defines some genera of Apseudomorpha and Paratanaidomorpha (e.g. *Pseudoapseudomorpha* and *Makraleptochelia*)

17 Uropodal endopod article 1 with fine mid-lenght setae (0 = absent, 1 = present). This character is a novel; it is found in males of neotanaidomorphans and should be considered in the future (e.g. *Neotanais bicornutus* Araújo-Silva et al., 2015: 538; fig. 1I and *Venusticrus thor* Araújo-Silva et al., 2015: 548; fig. 6C).

18 Type of reproduction (0 = gonoristic; 1 = hermaphoditic, 2 = male unknown). This character was added here due to the simultaneous hermaphoditism found in the species of genus *Apseudes*. Although the reproduction modes within tanaidaceans are still controversial, this character should be considered in the future since the reproduction is a very important issue within tanaidaceans.

19 Pleon short compared to the body length (≤20%) (0 = absent, 1 = present). This character is found mainly in the males and is here defining some species within Paratanaidomorpha.

20 Cheliped propodus distal margin long and curved (0 = absent, 1 = present). This character despite polymorphic occurs in the genus *Venusticrus* (suborder Neotanaidomorpha).

21 Cheliped propodus ventral setae type (0 = simple; 1 = bipinnate). This character defines some genera in Akanthophoreidae.

22 Cheliped carpus setae type (0 = absent; 1 = simple; 2 = plumose). Outgroup-defining character.

23 Eyes (0 = absent, 1 = present). This character corresponds to characters ‘8’ and ‘0’ from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

24 Cephalothorax narrowing anteriorly (0 = absent, 1 = present). This character corresponds to characters ‘9’ and '1' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

25 Pereon short and stout l/w ratio < 2.5 (0 = absent, 1 = present). This character corresponds to characters ‘11’ and '2' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively. This character is typically seen in Pseudotanaidae, certain species of Typhlotanaidae.

26 Pereonites 1–3 very short relative to pereonites 4–6 (0 = absent, 1 = present). This character corresponds to characters ‘12’ and ‘3’ from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively. This character is mainly seen in the family Pseudotanaidae.

27 Pereonite 1 hyposphenian/sternal spur (0 = absent, 1 = present). This character corresponds to characters ‘14’ and '5' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

28 Pleon fusion (any type) (0 = absent, 1 = present). This character corresponds to characters ‘9’ and '7' from Larsen & Wilson (2002) and Larsen & Araújo-Silva (2014), respectively. This character is found in the families Tanzanapseudidae, Synapseudidae, Metapseudidae and some paratanaoidean taxa, as well as the outgroup (i.e. isopods).

29 All pleonites narrower than pereon (0 = absent, 1 = present). This character corresponds to characters ‘6’ and '8' from Larsen & Wilson (2002) and Larsen & Araújo-Silva (2014), respectively.

30 Pleon partially reduced (0 = absent, 1 = present). This character corresponds to characters ‘15’ and '9' from Bird & Larsen (2009) and Larsen & Araújo-Silva

(2014), respectively. The present state is found in the family Tanaididae and Pseudozeuxidae.

31 Pleonite lateral plumose or circumplumose setae (0 = absent, 1 = present). This character corresponds to characters ‘16’ and '10' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

32 Pleonite 5 posteriorly directed ventral spur (0 = absent, 1 = present). The present state herein is restricted to the genus *Chauliopleona*, but it is also found in less degree in *Portaratrum* and some male species of the genus *Neotanais.*

33 Antennule short penultimate article (peduncle) (0 = absent, 1 = article 2, 2 = article 3). This character corresponds to characters ‘20’ and '14' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

34 Antennule minute, cap-like, terminal article (0 = absent, 1 = present). This character corresponds to characters ‘21’ and '15' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

35 Antenna multi-articled, count (0 = seven or more, 1 = six, 2 = less than six). This character corresponds to character ‘26’ and ‘17’ from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

36 Antenna article 2 dorsal strong acute spiniform seta/apophysis (0 = absent, 1 = present). This character corresponds to characters ‘29’ and '19' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

37 Antenna article 2 ventral strong acute spiniform or apophysis (spine) seta (0 = absent, 1 = apophysis; 2= spiniform seta). This character corresponds to characters ‘31’ and '21' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

38 Antenna article 3 dorsal strong acute spiniform or apophysis (spine) seta (0 = absent, 1 = apophysis; 2= spiniform seta). This character corresponds to characters ‘32’ and ‘22’ from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

39 Antenna article 3 strong broad-based spiniform ventral seta (0 = absent, 1 = present). This character corresponds to character ‘33’ and ‘23’ from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

40 Labial lobes (0 = two pairs, 1 = one pair; 2 = absent). This character corresponds to characters ‘34’ and ‘24’ from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

41 Labial spiniform medial seta (0 = absent, 1 = present). This character corresponds to character ‘25’ from Larsen & Araújo-Silva (2014). Within suborder Paratanaidomorpha, the present state is mainly found in the family Agathotanaidae, and in the recently described genus *Cheliasetosatanais*. Apparently, this character is also found in both Neotanaidomorpha and Apseudomorpha, but to a lesser degree (e.g. *Neotanais bicornutus* Araújo-Silva *et al*., 2015: 539; fig. 2H; *Apseudes noronhensis* Araújo-Silva *et al*., 2013: 229; fig. 4C).

42 Mandible molar broad or with grinding surface (0 = absent, 1 = present). This character corresponds to characters ‘35’ and ‘26’ from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

43 Mandible molar shape (0 = grinding, 1 = broad nodulose/setose, 2 = broad spinose, 3 = acuminate-armed, 4 = acuminate-simple, 5 = reduced/absent). This character corresponds to characters ‘36’ and '27' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

44 Mandible right incisor bifid – points open/symmetrical, with distal crenulations (0 = absent, 1 = present). This character corresponds to characters ‘37’ and '28' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

45 Mandible right incisor bifid – points closed/asymmetrical (0 = absent, 1 = present). This character corresponds to characters ‘38’ and '29' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

46 Mandible left incisor/lacinia broad, facing anterior (0 = absent, 1 = present). This character corresponds to character ‘39’ and '30' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

47 Maxilla modified (0 = absent [reduced/ovoid], 1 = present [developed]. This character corresponds to character '33' from Larsen & Araújo-Silva (2014). The present (and developed) state defines both Neotanaidomorpha and Apseudomorpha suborders. While in most Paratanaidomorpha families the absent state is found. A number of genera within the Tanaididae and Akanthophoreidae have a much better developed maxilla with a broad basis, and herein was scored as present, but in the future this character should be closely evaluated. The present state is also found in the isopod outgroup.

48 Maxilliped basis fusion (0 = absent, 1 = present). This character corresponds to characters ‘43’ and '35' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

49 Maxilliped endites distally expanded or flared (0 = absent, 1 = weak, 2 = strong, 3 = highly developed). This character corresponds to characters ‘45’ and '37' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

50 Maxilliped endite with medial coupling hooks (0 = absent, 1 = present). The presence state defines the suborder Apseudomorpha and is also found in the isopod outgroup.

51 Maxilliped endite large lateral seta (0 = absent, 1 = present). This character corresponds to characters ‘49’ and '41' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

52 Maxilliped basal setae count (0 = three or more, 1 = two, 2 = one, 3 = absent). This character corresponds to characters ‘50’ and '42' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

53 Maxilliped palp article 2 with bifid/trifid/strongly pectinate spiniform seta (0 = absent, 1 = present). This character corresponds to character ‘52’ and '44' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

54 Maxilliped palp article 2 long seta (as long as articles 3–4) (0 = absent, 1 = present). This character corresponds to characters ‘53’ and '45' from Bird & Larsen (2009) and Larsen & Araújo-Silva (2014), respectively.

55 Cheliped-cephalothorax sclerite dorsally inserted (triangular) on basis (0 = absent, 1 = present). This character corresponds to characters ‘56’ from Bird & Larsen (2009) and ‘38’ from Larsen & Wilson (2002).

56 Cheliped basis reaches pereonite 1 (0 = absent, 1 = present). This character corresponds to character ‘58’ from Bird & Larsen (2009).

57 Cheliped exopod (0 = absent, 1 = present). This character defines the suborder Apseudomorpha.

58 Cheliped carpus shield (0 = absent, 1 = present). This character corresponds to character ‘51’ from Larsen & Araújo-Silva (2014).

59 Cheliped carpus mid-ventral setae count (0 = four or more, 1 = three, 2 = two, 3 = one, 4 = absent). The state '0' is found herein in most of Apseudomorpha and the isopod outgroup.

60 Cheliped carpus multiple dorsal setae (0 = absent, 1 = present). The present state is found here in the neotanaidomorphans and some genera of apseudomorphans (e.g. *Mesokalliapseudes*).

61 Cheliped chela with elongated fixed finger and dactylus (0 = absent, 1 = present). This character corresponds to character ‘55’ from Larsen & Araújo-Silva (2014).

62 Cheliped fixed-finger crushing incisive margin (0 = absent, 1 = present). This character corresponds to character ‘62’ from Bird & Larsen (2009).

63 Cheliped propodus ventral setae count (0 = three or more, 1 = two, 2 = one; 3 = absent). This character corresponds to character ‘65’ from Bird & Larsen (2009).

64 Pereopod 1 spiniform coxa (0 = absent, 1 = present). The present state herein defines the family Apseudidae, but still brings some controversy, since is found in some genus of Kalliapseudidae as well (e.g. *Acutihumerus* Guţu, 2006).

65 Pereopod 1 exopod (0 = absent, 1 = present). Similarly to the characters '64' and '57', the present state herein defines the family Apseudidae.

66 Pereopod 1 bayonet spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘69’ from Bird & Larsen (2009).

67 Pereopod 1 propodus with ventrodistal type setation (0 = absent, 1 = simple seta, 2 = spiniform seta). This character corresponds to character ‘70’ from Bird & Larsen (2009).

68 Pereopod 1 dactylus/unguis clearly longer than propodus (0 = absent, 1 = present). This character corresponds to character ‘71’ from Bird & Larsen (2009).

69 Pereopod 1 unguis longer than dactylus (0 = absent, 1 = present). This character corresponds to character ‘72’ from Bird & Larsen (2009).

70 Pereopod 1 and pereopods 2–3 different in shape and setal arrangement (0 = absent/weak, 1 = moderate, 2 = strong). This character corresponds to character ‘73’ from Bird & Larsen (2009).

71 Pereopods 2–3 merus bayonet spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘75’ from Bird & Larsen (2009).

72 Pereopods 2–3 carpus bayonet spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘76’ from Bird & Larsen (2009).

73 Pereopods 2–3 carpus blade-like spiniform setae (0 = absent, 1 = present). This character corresponds to character ‘77’ from Bird & Larsen (2009). This character is exclusively found in the family Pseudotanaidae.

74 Pereopods 2–3 carpus spiniform setae count (0 = absent, 1 = one, 2 = two or more). This character corresponds to character ‘78’ from Bird & Larsen (2009).

75 Pereopods 2–3 carpus two ventrodistal spiniform setae (0 = absent; 1 = present, one type; 2 = present, two types). This character corresponds to character ‘81’ from Bird & Larsen (2009).

76 Pereopods 2–3 propodus ventrodistal seta (0 = absent, 1 = simple seta, 2 = spiniform seta, 3= bipinnate, pinnate or plumose). This character corresponds to character ‘79’ from Bird & Larsen (2009).

77 Marsupium structure (0 = four pairs, 1 = one pair 2 = ovisac). This character corresponds to character ‘41’ from Larsen & Wilson (2002). This character herein defines the suborder Tanaidomorpha (family Tanaididae) that bears an ovisac instead of one pair (family Pseudotanaidae).

78 Pereopods 4–6 coxa (0 = absent, 1 = present). This character corresponds to characters ‘47’ and '74' from Larsen & Wilson (2002) and Larsen & Araújo-Silva (2014), respectively.

79 Pereopods 4–6 basis stout (≤ 2.5 times longer than broad) (0 = absent, 1 = present). This character corresponds to character ‘84’ from Bird & Larsen (2009).

80 Pereopods 4–6 merus spine (0 = absent, 1 = simple, 2 = robust, 3 = bayonet). This character corresponds to character ‘85’ from Bird & Larsen (2009).

81 Pereopods 4–6 carpus microtrichial field or ‘prickly tubercle’ (0 = absent, 1 = microtrichia, 2 = microtrichia, strong, 3 = prickly tubercle). This character corresponds to character ‘86’ from Bird & Larsen (2009).

82 Pereopods 4–6 carpus bayonet setae (0 = absent, 1 = present). This character corresponds to character ‘87’ from Bird & Larsen (2009).

83 Pereopods 4–6 carpus complex-denticulate, or hook-like, spiniform setae (0 = absent, 1 = complex, 2 = hooks). This character corresponds to character ‘88’ from Bird & Larsen (2009).

84 Pereopods 4–6 carpus blade-like setae (0 = absent, 1 = present). This character corresponds to character ‘89’ from Bird & Larsen (2009). Similarly to character '73', here the present state defines genus *Pseudotanais*.

85 Pereopods 4–6 carpus spiniform setae count (0 = one, 1 = two, 2 = three, 3 = four or more, 4 = absent). This character is modified from character ‘90’ in Bird & Larsen (2009).

86 Pereopods 4–6 dorsomedial pinnate setae (0 = absent, 1 = present). This character corresponds to character ‘91’ from Bird & Larsen (2009).

87 Pereopods 4–5 propodus dorsodistal setae count (0 = four or more, 1 = three, 2 = two, 3 = one). This character corresponds to character ‘92’ from Bird & Larsen (2009).

88 Pereopod 6 propodus dorsodistal setae count (0 = four or more, 1 = three, 2 = two, 3 = one). This character corresponds to character ‘96’ from Bird & Larsen (2009).

89 Pereopods 4–6 rod, or bone-like seta (0 = absent, 1 = present). This character corresponds to character ‘98’ from Bird & Larsen (2009).

90 Pereopods 4–6 dactylus-unguis ‘claw-like’ (0 = absent, 1 = present). This character corresponds to character ‘99’ from Bird & Larsen (2009).

91 Pereopods 4–6 unguis tip modified (0 = absent, 1 = present). This character corresponds to character ‘100’ from Bird & Larsen (2009).

92 Pleopod basal article inner setae (0 = absent/reduced, 1 = present). This character corresponds to character ‘102’ from Bird & Larsen (2009).

93 Pleopodal endopod setae all terminal (0 = absent/reduced, 1 = present). This character corresponds to character ‘103’ from Bird & Larsen (2009).

94 Pleopodal exopod setae all terminal (0 = absent/reduced, 1 = present). This character corresponds to character ‘104’ from Bird & Larsen (2009).

95 Pleopodal endopod inner/subterminal setae count (0 = absent/reduced, 1 = one, 2 = two or more). This character corresponds to character ‘105’ from Bird & Larsen (2009).

96 Uropod (0 = biramous, 1 = uniramous). The '1' state defines the suborder Tanaidomorpha, despite the genus *Parafilitanais* here shows this state as well, but it should be verified in the future to check if is just reduced (as in Agathotanaidae).

97 Uropodal endopod articles count (0 = five or more, 1 = three to four, 2 = two, 3 = one, 4 = fused with basal article). This character corresponds to character ‘106’ from Bird & Larsen (2009).

98 Uropodal exopod articles count (0 = five or more, 1 = three to four, 2 = two, 3 = one, 4 = fused with basal article; 5 = absent). This character is modified from character '97' in Larsen & Araújo-Silva (2014).

99 Uropodalal exopod fused with basal article (0 = absent, 1 = present and naked, 2 = present and with setae). This character corresponds to character '95' from Larsen & Araújo-Silva (2014).

100 Uropodal endopod length (0 = longer than pleotelson, 1 = shorter than pleotelson; 2= as long as pleotelson). This character corresponds to character '98' from Larsen & Araújo-Silva (2014).

101 Uropodal endopod thin (≥ 3.5 times) (0 = absent, 1 = present). This character corresponds to character '99' from Larsen & Araújo-Silva (2014).

102 Uropodal exopod length (0 = longer than first endopod article, 1 = shorter than first endopod article, 2 = fused to basal article, 3= absent; 4 = exopod as long as endopod article 1). This character corresponds to character '100' from Larsen & Araújo-Silva (2014).

103 Uropodal basal article [with exopod] spur (0 = absent, 1 = present). This character corresponds to character '102' from Larsen & Araújo-Silva (2014).

104 Non-feeding male (0 = absent, 1 = present, 2= unknown). This character corresponds to a restricted form of character '4' from Larsen & Wilson (2002).

105 Maxilliped palp article 2 medial setae count (0 = four or more, 1 = three, 2 = two; 3 = one; 4 = absent). This character corresponds to character '54' from Bird & Larsen (2009).

106 Maxilliped palp article 3 medial setae count (0 = five or more, 1 = three or four; 2 = two or one; 3 = absent). This character corresponds to character '55' from Bird & Larsen (2009).

107 Antenna article 2 dorsal stout broad-based spiniform seta (0 = absent, 1 = present). This character corresponds to character '30' from Bird & Larsen (2009).

108 Antennule article count (0 = six or more, 1 = four or five 2 = three). The '0' state defines the suborders Apseudomorpha and Neotanaidomorpha. It is also found in the outgroup.

109 Mandibular palp articles (0 = absent; 1 = one; 2 = three). This character defines the suborder Apseudomorpha and outgroup.

110 Rostrum shape (0 = absent; 1 = strong; 2 = slight/weak). This character defines the suborder Apseudomorpha and outgroup.

111 Mandible palp (0 = absent, 1 = present). This character defines the suborder Apseudomorpha and outgroup.

112 Genital cones (0 = one; 1 = two). This character defines the suborders of Tanaidacea.

Appendix III. Character matrix data corresponding to the morphological phylogenetic analyses presented in Chapter III, **Article 7**.

Taxa/Characters	1–10	11–20	21–30	31–40	41–50	51–60
Leptochelia	1000000110	0001110100	0110000000	0001111100	0101000000	100010001[01]
Leviapseudes	100001[01]000	1101010[01]00	0100001010	0000000001	1110001001	0301001000
Pseudoapseudomorpha	100000000[01]	1110020010	0[12]10000010	1000000001	1120001001	120[01]0010[12]0
Mesokalliapseudes	0000000000	1000310000	0200000000	1000000001	0110001001	0000000001
Zeuxo	1000000110	1101110000	0110100001	1001000001	0110000000	0200110000
Tanais	1000000110	0001010[01]00	0110100001	1001000001	0110000000	0000110020
Collettea	1000000110	0000400000	0100000000	0021100001	0020000110	03001000[234]0
Parafilitanais	0000000110	0000310000	0100000000	0020100001	0030000110	03000000[23]0
Chauliopleona	1000000110	0001310200	0100000000	0121100001	0030001100	121[01]1001[23]0
Stenotanais	0000000110	0001310010	[01]100000000	0020100001	0040001110	02001001[23]0
Leptognathiella	1000000110	0000310010	0100000000	0001200001	00[34]0000110	0[23]00100030
Biarticulata	1000000110	0001310000	0100000000	0021100001	0040000110	03001000[23]0
Arhaphuroides	0000000110	11003100[01]0	0100000000	0020100001	0030000110	0[23]00100020
Paraiungentitanais	00?1000110	????310200	0100100000	000010000?	?01000???0	????100020
Venusticrus	100000[01]110	0001[03]11001	0100000000	10?0000000	1120001000	0100110021
Pseudotanais	0000100110	0001310010	01[01]1110000	0000110001	00301101[13]0	0200000020
Nototanais	1000000110	0000310000	0111000000	0000100001	0111010110	0201110010
Typhlotanais	1000000110	0001310000	0100000000	0010100001	0020000110	0[23]0000001[01]
Insociabilitanais	0000000110	0000400000	0100001000	002020000?	?110000110	0300000020
Caudalonga	1000000110	0000210210	0100000010	0020100001	0040000100	0?10100040
Paragathotanais	0000000110	0000310010	0100000000	0020200001	1040000110	03000000[23]0
Armaturatanais	1000000110	0000400010	0100000000	0000100001	0110000100	03001100[23]0
Cheliasetosatanais	1000001110	0001310010	0100000000	0001110101	1030000100	1200100020
Asellus	00-0000110	1101011010	0010100111	0000000002	-121001001	00000-0001
Idotea	00-0000110	0000011010	0010[01]00101	0000000002	-111001001	02000-0000
Acanthocope	10-0000111	1101211010	0000110100	0010001002	-020101001	00000-0020

...continued on the next page..

Appendix III. *(continued)*

Taxa/Characters	61–70	71–80	81–90	91–100	101–110	111–112
Leptochelia	0[01][01]0001101	000[12][01][12]0011	10002000[01]1	1100200[23]00	1[01]01001100	01
Leviapseudes	1001102002	00001[12]0100	000020300[01]	11[01][01][01]00000	1000000021	10
Pseudoapseudomorpha	[01]000002000	000202010[01]	0000301001	0000000000	1000000022	10
Mesokalliapseudes	0020002002	0002110110	0000000001	1100100100	1000000011	10
Zeuxo	0000001012	000211211[12]	1010[23]00001	0100210500	1300200100	01
Tanais	0100001002	000221210[12]	101030[03]001	0100212500	1300000100	01
Collettea	00[12]000[02]0[01]0	000[12][012][12]01[01]1	0100303[023][01]1	0[01]00002301	[01]101[01]10100	01
Parafilitanais	0010002010	000[01]0[03]?101	0[01]00303301	0011012500	10001[12]0100	01
Chauliopleona	0010012000	[01]1021200[01]1	0100[23]03[01]11	0001102201	1101[01]10100	01
Stenotanais	0010012000	11021200[01]1	0100203[12]11	0000202300	1000[12][01]0100	01
Leptognathiella	0010012[01][01]0	1102[01]20001	0100203[23]0[01]	0011002[23]0[01]	1[01][01]0110100	01
Biarticulata	0010012000	1102120001	0100203201	0000102200	1101[12]10100	01
Arhaphuroides	0010012[01]10	1[01]022[23]0101	0100[23]13[12]01	00[01][01]00[23]421	1110110100	01
Paraiungentitanais	1010011000	0?????0000	0000202?01	10???02200	110???0100	01
Venusticrus	0010012001	0002130101	0000301000	1100200200	1101000000	01
Pseudotanais	1020001012	0012021101	00011[01]3301	0011002200	1001111200	01
Nototanais	0120000011	0002120001	0100303101	1000202201	1001111200	01
Typhlotanais	1[01]10001011	000[12][01][23]00[01]1	3020013101	[01]00020220[01]	1001110200	01
Insociabilitanais	0010001110	100212?001	0100203300	0011002302	1100110100	01
Caudalonga	0010011010	1102010101	0100203301	0000002422	1202110100	01
Paragathotanais	0[01]2001[12]0[01]0	1102[12]20101	0100213[12]00	0011003421	02001[12]0100	01
Armaturatanais	001000[12]010	010[12]02?101	0[01]00303200	0000202101	0100[23]20100	01
Cheliasetosatanais	0010002010	0102120101	0000303110	0000202201	1000011100	01
Asellus	- -300- - - - -	0002?[12]?111	-00030?001	0- - - -03320	1400000020	10
Idotea	- -000-[12]- -1	000??0?10?	- -00?0??0?	110021?501	1000410100	00
Acanthocope	- -100-0- -0	0000?1?100	-000000000	1- - - -13500	1000330020	10

Appendix IV. List of Tanaidacea species/genera identified in this thesis from the REVIZEE-NE Program with its geographic distribution. Abbreviations: SO = Southern Ocean (Antarctic and Subantarctic); SA = South Atlantic; NA= North Atlantic; SP = South Pacific; CP = Central Pacific; NP = North Pacific; IO = Indian Ocean; GoM = Gulf of Mexico; Bc = Brazilian coast. * New species/genera described; ** New record.

Taxa	Geographic distribution
Suborder Apseudomorpha Sieg, 1980	
Family Apseudidae Leach, 1813	
Genus *Apseudes* Leach, 1813**	SO, SA (Bc**), NA, Mediterranean, GoM, NP, SP, IO
Apseudes aisoe Araújo-Silva *et al*. 2013*	SA (Bc)
Apseudes noronhensis Araújo-Silva *et al*. 2013*	SA (Bc)
Genus *Paradoxapseudes* Guţu, 1991	
Paradoxapseudes cf. *intermedius*	SA, NA
Suborder Paratanaidomorpha Lang, 1949	
Family Tanaellidae Larsen & Wilson, 2002	
Genus *Arhaphuroides* Sieg, 1986 **	SO, SA (Bc**), NA, GoM, SP, NP
Arhaphuroides sp.	
Family Leptognathiidae Sieg, 1976**	
Genus *Biarticulata* Larsen & Shimomura, 2007**	SA**, SP, NP, IO, Arctic
Biarticulata sp.	
Family Leptocheliidae Lang, 1973	
Genus *Intermedichelia* Guţu, 1996	SA (endemic for Bc so far)
Intermedichelia gracilis Guţu, 1996	
Intermedichelia jesseri Araújo-Silva & Larsen 2012a*	
Genus *Makraleptochelia* Araújo-Silva & Larsen, 2012a*	SA
Makraleptochelia potiguara Araújo-Silva & Larsen, 2012a*	
Family Paratanaidae Lang, 1949	
Genus *Paratanais* Dana, 1852	SO, SA, NA, Mediterranean, NP, SP, IO
Paratanais coelhoi Araújo-Silva & Larsen, 2012b*	SA
Family Nototanaidae Sieg, 1976**	
Genus *Nototanoides* Sieg & Heard, 1985**	
Nototanoides cf. *trifurcatus* Sieg & Heard, 1985**	SA**, NA, GoM

Appendix V. List of Tanaidacea species/genera identified in this thesis from the ANDEEP I-III Campaigns with its geographic distribution. Abbreviations: SO = Southern Ocean (Antarctic and Subantarctic); SA = South Atlantic; NA= North Atlantic; SP = South Pacific; CP = Central Pacific; NP = North Pacific; IO = Indian Ocean; GoM = Gulf of Mexico. * New species/genera described; ** New record.

Taxa	Geographic distribution
Suborder Apseudomorpha Sieg, 1980	
Family Apseudidae Leach, 1813	
Genus *Apseudes* Leach, 1813	SO, SA, NA, Mediterranean, GoM, NP, SP, IO
Apseudes sp.	
Genus *Leviapseudes* Sieg, 1983	SO, SA, NA, GoM, SP, IO
Leviapseudes sp.	
Suborder Neotanaidomorpha Sieg, 1980	
Family Neotanaidae Lang, 1956	
Genus *Neotanais* Beddard, 1886	SO, SA, NA, GoM, SP, NP, IO, Arctic
Neotanais bicornutus Araújo-Silva & Larsen, 2015*	SO
Suborder Paratanaidomorpha Lang, 1949	
Family Tanaellidae Larsen & Wilson, 2002	
Genus *Araphura* Bird & Holdich, 1984	SO, SA, NA, GoM, SP, NP
Araphura sp. A	
Araphura sp. B	
Genus *Tanaella* Norman & Stebbing, 1886	SO, SA, NA, GoM, SP, NP, Arctic
Tanaella cf. *kroyeri* Larsen & Araújo-Silva, 2009 **	SO**, SA (deep-sea of Brazil)
Tanaella cf. *prolixcauda* Larsen & Heard, 2004 **	SO**, GoM
Tanaella sp.	
Family Paratanaoidea incertae sedis Larsen & Wilson, 2002	
Genus *Armaturatanais* Larsen, 2005 **	SO**, NA, GoM
Armaturatanais sp.	
Genus *Exspina* Lang, 1968	SO, NA, SP
Exspina typica Lang, 1968	SO, NA, SP
Genus *Parafilitanais* Kudinova-Pasternak, 1989 **	SO**, NA, GoM, SP, IO
Parafilitanais sp.	
Genus *Portaratrum* Guerrero-Kommritz, 2003 **	SO**, SA
Portaratrum sp.	
Genus *Robustochelia* Kudinova-Pasternak, 1983	
Robustochelia sp.	SO, NA, GoM, CP, IO

Family Colletteidae Larsen & Wilson, 2002	
Genus *Collettea* Lang, 1973	SO, SA, NA, GoM, SP, CP, IO, Arctic
Collettea sp.	
Family Agathotanaidae Lang, 1971	
Genus *Agathotanais* Hansen, 1913	SO, SA, NA, GoM, SP, CP, NP, IO
Agathotanais sp.	
Genus *Paragathotanais* Lang, 1971	SO, SA, NA, GoM, SP, NP, IO
Paragathotanais sp. A	
Paragathotanais sp. B	
Paragathotanais sp. C	
Genus *Paranarthrura* Hansen, 1913	SO, SA, NA, GoM, SP, NP, IO, Arctic
Paranarthrura cf. *angolensis* Guerrero-Kommritz *et al*., 2002**	SA (Angola Basin) and SO**
Paranarthrura fortispina Sieg, 1986	SO
Paranarthrura sp.	
Family Pseudotanaidae Sieg, 1976	
Genus *Pseudotanais* Sars, 1882a	SO, SA, NA, GoM, SP, NP, IO, Arctic
Pseudotanais sp. A	
Pseudotanais sp. B	
Family Typhlotanaidae Sieg, 1984	
Genus *Insociabilitanais* Larsen, 2005 **	SO**, GoM
Insociabilitanais sp.	
Genus *Meromonakantha* Sieg, 1986	SO, NA, GoM, SP, NP, Arctic
Meromonakantha sp.	
Genus *Typhlotanais* Sars, 1882	SO, NA, Mediterranean, SP, CP, NP, IO, Arctic
Typhlotanais sp. A	
Typhlotanais sp. B	
Typhlotanais sp. C	
Family Leptognathiidae Sieg, 1976	
Genus *Leptognathia* Sars, 1882	SO, SA, NA, GoM, SP, NP, IO, Arctic
Leptognathia sp.	
Family Akanthophoreidae Sieg, 1986	
Genus *Akanthophoreus* Sieg, 1986	SO, SA, NA, Mediterranean, SP, NP, IO, Arctic
Akanthophoreus sp.	
Genus *Chauliopleona* Dojiri & Sieg, 1997	SO, SA, NA, GoM, SP, NP, IO, Arctic
Chauliopleona ciimari Larsen & Araújo-Silva 2014 *	SO

Chauliopleona andeepi Larsen & Araújo-Silva 2014 *	
Chauliopleona nickeli Guerrero-Kommritz 2005	SO
Genus *Parakanthophoreus* Larsen & Araújo-Silva 2014 *	SO, SA, NA, NP, Arctic
Parakanthophoreus greenwichius Larsen & Araújo-Silva 2014 *	SO
Genus *Stenotanais* Bird & Holdich, 1984	SO, NA, GoM, CP
Stenotanais sp.	
Family Anarthruridae Lang, 1971	
Genus *Arthrura* Kudinova-Pasternak, 1966	SO, GoM, SP, NP
Arthrura pulcher (Lang, 1971)	SO, SP

Appendix VI. List of Tanaidacea species/genera identified in this thesis from the BIONOD/2012 Campaign with its geographic distribution. Abbreviations: SO = Southern Ocean (Antarctic and Subantarctic); SA = South Atlantic; NA= North Atlantic; SP = South Pacific; CP = Central Pacific; NP = North Pacific; IO = Indian Ocean; GoM = Gulf of Mexico. *New species/genera described; ** New record.

Taxa	Geographic distribution
Suborder Apseudomorpha Sieg, 1980	
Family Apseudidae Leach, 1813	
Genus *Carpoapseudes* Lang, 1968	SA, NA, NP, IO
Carpoapseudes sp.	
Genus *Leviapseudes* Sieg, 1983 **	SO, SA, NA, GoM, SP, NP**, IO
Leviapseudes sp. A	
Leviapseudes sp. B	
Genus *Glabroapseudes* Guerrero-Kommritz & Heard, 2003 **	SO, SA, IO, NP**
Glabroapseudes sp.	
Suborder Neotanaidomorpha Sieg, 1980	
Family Neotanaidae Lang, 1956	
Genus *Neotanais* Beddard, 1886	SO, SA, NA, GoM, SP, NP, IO, Arctic
Neotanais sp.	
Genus *Venusticrus* Gardiner, 1975 **	NA, NP**
Venusticrus thor Araújo-Silva & Larsen, 2015 *	
Suborder Paratanaidomorpha Lang, 1949	
Family Cryptocopidae (McLelland, 2008) Bird & Larsen, 2009	
Genus *Cryptocopoides* (Sieg, 1973) Sieg, 1976	SO, NA, NP, Arctic
Cryptocopoides cf. *pacificus* McLelland, 2007	NP
Genus *Paraiungentitanais* Sieg, 1977 **	SO, NP**
Paraiungentitanais sp.	
Family Tanaellidae Larsen & Wilson, 2002	
Genus *Araphura* Bird & Holdich, 1984	SO, SA, NA, GoM, SP, NP
Araphura sp.	
Genus *Arhaphuroides* Sieg, 1986	SO, SA, NA, GoM, SP, NP
Arhaphuroides sp.	
Genus *Tanaella* Norman & Stebbing, 1886	SO, SA, NA, GoM, SP, NP, IO
Tanaella sp.	
Family Paratanaoidea *incertae sedis* Larsen & Wilson, 2002	
Genus *Armaturatanais* Larsen, 2005 **	SO, NA, GoM, NP**

Armaturatanais sp.	
Genus *Caudalonga* Larsen, 2005**	GoM, NP**
Caudalonga sp.	
Genus *Parafilitanais* Kudinova-Pasternak, 1989 **	SO, NA, GoM, SP, NP**, IO
Parafilitanais sp.	
Genus *Portaratrum* Guerrero-Kommritz, 2003 **	SO, SA, SP, NP**
Portaratrum sp.	
Family Colletteidae Larsen & Wilson, 2002	
Genus *Cheliasetosatanais* Larsen & Araújo-Silva 2014*	NP
Cheliasetosatanais spinimaxillipedus Larsen & Araújo-Silva 2014*	
Genus *Collettea* Lang, 1973	SO, SA, NA, GoM, SP, NP, IO, Arctic
Collettea sp.	
Genus *Leptognathiopsis* Holdich & Bird, 1986	NA, NP
Leptognathiopsis cf. *langi* (Kudinova-Pasternak, 1970)	NP
Genus *Leptognathiella* Hansen, 1913**	SO, NA, GoM, NP**, Arctic
Leptognathiella sp. A	
Leptognathiella sp. B	
Leptognathiella sp. C	
Genus *Tumidochelia* Knight *et al*., 2003	NA, GoM, NP
Tumidochelia sp.	
Family Agathotanaidae Lang, 1971	
Genus *Agathotanais* Hansen, 1913	SO, SA, NA, GoM, SP, CP, NP, IO
Agathotanais sp.	
Genus *Paragathotanais* Lang, 1971	SO, SA, NA, GoM, SP, NP, IO
Paragathotanais sp. A	
Paragathotanais sp. B	
Paragathotanais sp. C	
Genus *Paranarthrura* Hansen, 1913	SO, SA, NA, GoM, SP, NP, IO, Arctic
Paranarthrura sp.	
Family Pseudotanaidae Sieg, 1976	
Genus *Pseudotanais* Sars, 1882	SO, SA, NA, GoM, SP, NP, IO, Arctic
Pseudotanais sp. A	
Pseudotanais sp. B	
Family Typhlotanaidae Sieg, 1984	
Genus *Insociabilitanais* Larsen, 2005 **	SO, GoM, NP**

Insociabilitanais sp.	
Genus *Larsenotanais* Błażewicz-Paszkowycz, 2007	
Larsenotanais sp.	SO, NA, NP
Genus *Meromonakantha* Sieg, 1986	SO, NA, GoM, SP, NP, Arctic
Meromonakantha sp.	
Genus *Paratyphlotanais* Kudinova-Pasternak & Pasternak, 1978**	SO, NA, SP, NP**
Paratyphlotanais sp.	
Genus *Pulcherella* Błażewicz-Paszkowycz, 2007**	SO, NA, NP**
Pulcherella sp.	
Genus *Typhlamia* Błażewicz-Paszkowycz, 2007	SO, NA, NP, Arctic
Typhlamia sp.	
Genus *Peraeospinosus* Sieg, 1986	SO, SP, NP, IO
Peraeospinosus sp.	
Genus *Typhlotanais* Sars, 1882	SO, NA, Mediterranean, SP, CP, NP, IO, Arctic
Typhlotanais sp. A	
Typhlotanais sp. B	
Family Leptognathiidae Sieg, 1976	
Genus *Biarticulata* Larsen & Shimomura, 2007	SP, NP, IO, Arctic
Biarticulata sp.	
Genus *Leptognathia* Sars, 1882	SO, SA, NA, GoM, SP, NP, IO, Arctic
Leptognathia sp.	
Family Akanthophoreidae Sieg, 1986	
Genus *Chauliopleona* Dojiri & Sieg, 1997	SO, SA, NA, GoM, SP, NP, IO, Arctic
Chauliopleona sp.	
Genus *Stenotanais* Bird & Holdich, 1984	SO, NA, GoM, NP
Stenotanais sp.	

Appendix VII. Character matrix data corresponding to the morphological phylogenetic analyses presented in the Chapter IV, heading 4.4 (Figure 54).

Taxa/Characters	1–10	11–20	21–30	31–40	41–50	51–60
Makraleptochelia (♀)	0110000110	0001010000	0110000000	0001100000	011100?000	0000110110
Makraleptochelia (♂)	0010000110	0000010010	0111000000	000-10000-	0- - - - - -000	-000110010
Intermedichelia	0001[01]00110	0001210000	0110000000	0001102000	011100?000	0[01]001100[12]0
Leptochelia	1000000110	0001110100	0110000000	0001111100	0101000000	100010001[01]
Apseudes	100001[01]00[01]	1010010100	011000[01]000	1000000001	1110001001	0000001000
Leviapseudes	100001[01]000	1101010[01]00	0100001010	0000000001	1110001001	0301001000
Pseudoapseudomorpha	100000000[01]	1110020010	0[12]10000010	1000000001	1120001001	120[01]0010[12]0
Mesokalliapseudes	0000000000	1000310000	0200000000	1000000001	0110001001	0000000001
Paratanais	1000000110	0001310000	0110000000	1021102201	0121000100	02001[01]0020
Zeuxo	1000000110	1101110000	0110100001	1001000001	0110000000	0200110000
Tanais	1000000110	0001010[01]00	0110100001	1001000001	0110000000	0000110020
Collettea	1000000110	0000400000	0100000000	0021100001	0020000110	03001000[234]0
Parafilitanais	0000000110	0000310000	0100000000	0020100001	0030000110	03000000[23]0
Chauliopleona	1000000110	0001310200	0100000000	0121100001	0030001100	121[01]1001[23]0
Stenotanais	0000000110	0001310010	[01]100000000	0020100001	0040001110	02001001[23]0
Parakanthophoreus	0000000110	0001310200	1100000000	0021100001	0030001110	0[23]10100130
Leptognathiella	1000000110	0000310010	0100000000	0001200001	00[34]0000110	0[23]00100030
Biarticulata	1000000110	0001310000	0100000000	0021100001	0040000110	03001000[23]0
Leptognathia	0000000110	00003100[01]0	0100000000	0020[12]00001	0040000110	02001000[23]0
Arhaphuroides	0000000110	11003100[01]0	0100000000	0020100001	0030000110	0[23]00100020
Paraiungentitanais	00?1000110	????310200	0100100000	000010000?	?01000???0	????100020
Venusticrus	100000[01]110	0001[03]11001	0100000000	10?0000000	1120001000	0100110021
Neotanais	100000[01]110	0001311[01]00	0100000000	[01]0?0000000	1120001000	0[12]0011002[01]
Pseudotanais	0000100110	0001310010	01[01]1110000	0000110001	00301101[13]0	0200000020
Nototanais	1000000110	0000310000	0111000000	0000100001	0111010110	0201110010
Typhlotanais	1000000110	0001310000	0100000000	0010100001	0020000110	0[23]0000001[01]
Insociabilitanais	0000000110	0000400000	0100001000	002020000?	?110000110	0300000020
Caudalonga	1000000110	0000210210	0100000010	0020100001	0040000100	0?10100040
Paragathotanais	0000000110	0000310010	0100000000	0020200001	1040000110	03000000[23]0
Armaturatanais	1000000110	0000400010	0100000000	0000100001	0110000100	03001100[23]0
Cheliasetosatanais	1000001110	0001310010	0100000000	0001110101	1030000100	1200100020
Asellus	00-0000110	1101011010	0010100111	0000000002	-121001001	00000-0001
Idotea	00-0000110	0000011010	0010[01]00101	0000000002	-111001001	02000-0000
Acanthocope	10-0000111	1101211010	0000110100	0010001002	-020101001	00000-0020

...continued on the next page..

Appendix VIII. (*Continued*).

Taxa/Characters	61–70	71–80	81–90	91–100	101–110	111–112
Makraleptochelia (♀)	0110001112	0000030011	0000[12]00001	0000101300	000?000102	01
Makraleptochelia (♂)	0010002000	000202-012	0000[12]00001	0000101300	0101- -0002	-1
Intermedichelia	0010000112	000[01]01001[12]	1010[12]02001	0100100[23]00	0101[01]00100	01
Leptochelia	0[01][01]0001101	000[12][01][12]0011	10002000[01]1	1100200[23]00	1[01]01001100	01
Apseudes	0001102002	01021[12]010[12]	0000201000	0100200000	1000000021	10
Leviapseudes	1001102002	00001[12]0100	000020300[01]	11[01][01][01]00000	1000000021	10
Pseudoapseudomorpha	[01]000002000	000202010[01]	0000301001	0000000000	1000000022	10
Mesokalliapseudes	0020002002	0002110110	0000000001	1100100100	1000000011	10
Paratanais	0100001011	00021100[01]2	2010[123]1[13]101	0000[01]02301	1001210100	01
Zeuxo	0000001012	000211211[12]	1010[23]00001	0100210500	1300200100	01
Tanais	0100001002	000221210[12]	101030[03]001	0100212500	1300000100	01
Collettea	00[12]000[02]0[01]0	000[12][012][12]01[01]1	0100303[023][01]1	0[01]00002301	[01]101[01]10100	01
Parafilitanais	0010002010	000[01]0[03]?101	0[01]00303301	0011012500	10001[12]0100	01
Chauliopleona	0010012000	[01]1021200[01]1	0100[23]03[01]11	0001102201	1101[01]10100	01
Stenotanais	0010012000	11021200[01]1	0100203[12]11	0000202300	1000[12][01]0100	01
Parakanthophoreus	0010012000	1102120001	0100[23]03311	0000202200	1101110100	01
Leptognathiella	0010012[01][01]0	1102[01]20001	0100203[23]0[01]	0011002[23]0[01]	1[01][01]0110100	01
Biarticulata	0010012000	1102120001	0100203201	0000102200	1101[12]10100	01
Leptognathia	00[12]00[01]2[01]10	1[01]02[01]20001	0100[123]02201	0000202301	1101210100	01
Arhaphuroides	0010012[01]10	1[01]022[23]0101	0100[23]13[12]01	00[01][01]00[23]421	1110110100	01
Paraiungentitanais	1010011000	0?????0000	0000202?01	10???02200	110???0100	01
Venusticrus	0010012001	0002130101	0000301000	1100200200	1101000000	01
Neotanais	0[01]100[01]2000	0002130100	0000301000	1100200[23]00	11[01]1000000	01
Pseudotanais	1020001012	0012021101	00011[01]3301	0011002200	1001111200	01
Nototanais	0120000011	0002120001	0100303101	1000202201	1001111200	01
Typhlotanais	1[01]10001011	000[12][01][23]00[01]1	3020013101	[01]00020220[01]	1001110200	01
Insociabilitanais	0010001110	100212?001	0100203300	0011002302	1100110100	01
Caudalonga	0010011010	1102010101	0100203301	0000002422	1202110100	01
Paragathotanais	0[01]2001[12]0[01]0	1102[12]20101	0100213[12]00	0011003421	02001[12]0100	01
Armaturatanais	001000[12]010	010[12]02?101	0[01]00303200	0000202101	0100[23]20100	01
Cheliasetosatanais	0010002010	0102120101	0000303110	0000202201	1000011100	01
Asellus	- -300- - - - -	0002?[12]?111	-00030?001	0- - - -03320	1400000020	10
Idotea	- -000-[12]- -1	000??0?10?	- -00?0??0?	110021?501	1000410100	00
Acanthocope	- -100-0- -0	0000?1?100	-000000000	1- - - -13500	1000330020	10